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# Energetical Significance of the Annelids and Arthropods in a Swedish Grassland Soil

T Persson & U Lohm

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# Energetical Significance of the Annelids and Arthropods in a Swedish Grassland Soil

T Persson & U Lohm

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# SERIES PREFACE

The International Biological Programme, through its section PT (productivity of terrestrial ecosystems), promoted a new type of interdisciplinary large scale ecosystem research in a number of biomes (desert, grassland, forest, tundra). Various biotic and abiotic factors were studied within these ecosystem projects, and particular emphasis was put on the energy flow through the ecosystem and its various trophic levels.

The Swedish Natural Science Research Council supported IBP/PT studies in grassland, forest and tundra, and the present volume contains some of the major results of the grassland investigations. This is probably one of the most detailed studies comprising a major part of the soil fauna carried out within IBP. The volume not only gives a detailed discussion on the individual species and other taxa but also a survey of feeding habits and functional importance of the different fauna groups. Comparisons are also made with other grassland ecosystems.

The scarcity of data on the soil fauna in various ecosystems and soil types makes the present volume important for all those interested in soil biology and soil processes. A large amount of work is obviously needed to complete a study like the present one, but it is hoped that this will not discourage but rather stimulate research on the soil fauna and its function in ecosystems.

Thomas Rosswall
Editor-in-Chief
*Ecological Bulletins*

## ABSTRACT

The abundance, biomass and respiratory metabolism were estimated for the individual species, larger taxa and feeding categories of the litter- and soil-inhabiting annelids and arthropods in an abandoned field. The sampling scheme covered one year, and the samplings were allocated in time and space in order to obtain unbiased mean estimates. About 250 species were treated separately, of which the collembolan *Tullbergia krausbaueri* dominated the abundance and the lumbricid *Allolobophora rosea* the biomass and respiration. The annual mean abundance of 247 000 (*s.e.* = 18 000) ind. $m^{-2}$ was dominated by Collembola (44 %) and Acari (43 %). The annual mean biomass of 10.6 (*s.e.* = 0.75) g dw $m^{-2}$ was dominated by Lumbricidae (56 %) and Coleoptera (27 %). The annual respiration of 200 (*s.e.* = 25) kcal $m^{-2}$ $yr^{-1}$ was also dominated by Lumbricidae (38 %), but Enchytraeidae (21 %), Coleoptera (21 %) and Diptera (15 %) contributed significantly to the total respiratory metabolism. Three feeding categories were distinguished, of which the saprovores/microbivores accounted for 75 %, the herbivores for 15 % and the carnivores for 10 % of the total annual respiration.

The net primary production, plant litter production and the rejecta and carcasses from the above-ground arthropods were also estimated in order to relate the soil animal respiration to various inputs of energy to the soil system. The results indicate that the litter- and soil-inhabiting annelids and arthropods contributed 6–7 % to the annual heterotrophic soil respiration. The significance of this contribution is discussed with regard to the energy flow through the ecosystem. The seasonal fluctuations in abundance and biomass are also discussed and compared with other grasslands. The study also includes a review of data on respiratory rates.

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# PREFACE

The aim of the present study is to give an account of the contribution by individual species to the below-ground annelid and arthropod abundance, biomass and respiratory metabolism in a grassland ecosystem and to provide a synthesis of this information in relation to other biotic components in the ecosystem.

We prefer to present the information in a monograph form so that information is available to provide the reader with the data base used for the conclusions. Owing to the different levels of detailedness, we recommend those who are interested in more general information to read the Introduction, the General discussion of Below-ground annelids and arthropods and the Synthesis. The most detailed and specific information is given in the presentation of each taxonomic group.

A number of people have assisted in different ways in this study. We are particularly grateful to Fil.mag. B. Vegerfors-Persson, who made many of the calculations, gave advice on the statistical treatment and made valuable suggestions on the manuscript. We are also very grateful to Dr. B. Axelsson, who took an active part in the planning and sampling and who has commented on major parts of the manuscript. We are also indebted to Dr. L. Hedström, who determined the adults of Orthoptera, Psocoptera, Thysanoptera, Cicadina, Heteroptera, Hymenoptera and Diptera; to Prof. A. Holm, who determined the Araneae; to Prof. J. Pettersson, who determined the Aphidina; and to Med.lic. O. Trottestam, who determined the adult Coleoptera. We also wish to thank Dr. D. Gärdefors, Dr. O. Tenow, and Dr. L. Wallin for active participation in the planning of the study.

Agr. P.-O. Johansson estimated the above-ground plant biomass in 1969 and 1970 and put the data at our disposal. Dr. H. Persson took part in developing a method of estimating rhizome production and also helped with the root sampling in 1971. Fil. mag. S. Larsson gave us permission to use unpublished data on respiration rates. Dr. H. Petersen (Molslaboratoriet, Denmark) put unpublished data at our disposal for calculation of Collembola biomasses and gave valuable suggestions to the manuscript. Lic. E. Bosatta assisted in various ways, and made, for example, the bomb-calorimetric measurements. Drs. F. Andersson, S. Håkansson, S. Nordström, J.E. Satchell (Grange-over-Sands, England), J.A. Wallwork (London, England), Fil.kand. T. Rosswall and Fil.kand. A. Wirén read parts of the manuscript and made important comments. Prof. B. Matérn and Prof. P. Seeger contributed with statistical advice, Fil.kand. N. Rollison corrected the English text, Mrs. I. Thomasson made the drawings, Mrs. G. Ivarsson typed the manuscript and Fil.mag. J. Enberg, among others, assisted in hand sorting soil samples. To all these persons we express our sincere gratitude.

We also wish to thank Prof. B. Kullenberg and Prof. K.-G. Nyholm for providing working facilities, and Prof. H. Sjörs who was one of the initiators of the studies in Central Sweden on Section PT of the Swedish contribution to the International Biological Programme, to which this study belongs. The field study was performed in an area belonging to Uppsala University. Grants for the study were received from the Swedish Natural Science Research Council and the Foundation for Zoological Research, Uppsala, which are gratefully acknowledged. Finally, we wish to express our gratitude to the Swedish Coniferous Forest Project for the considerable resources put at our disposal during the final phase of the study.

The design of the study, the performance of the field work and animal extractions, and the conclusions drawn are the result of a combined effort by the two authors. T. Persson made the species determination of Collembola, Acari and most insect larvae, and U. Lohm made the corresponding work on Enchytraeidae. T. Persson was responsible for the data on abundance, biomass and respiration of Lumbricidae and most arthropod taxa, while both authors were responsible for the data on the primary producers, Enchytraeidae and Coleoptera. The manuscript was prepared primarily by T. Persson, but both authors are responsible for the final version,

March, 1977

Tryggve Persson Ulrik Lohm

**Department of Entomology, Uppsala University,**
**Box 561, S–751 22 Uppsala, Sweden**

# INTRODUCTION

## BACKGROUND

This work was performed as a grassland study within the International Biological Programme (IBP), whose overall purpose was to examine "the biological basis of productivity and human welfare" on a world-wide scale. Temperate and tropical grasslands together comprise about 16 % of the earth's land surface and are also responsible for about 16 % of the net primary production on land, or 11 % of the total world net primary production (Whittaker & Likens, 1975). The Swedish grasslands mainly consist of hay-land and pastures, but during recent decades abandoned land has become a quantitatively important element in the Swedish landscape. In Sweden, abandonment of farm land will sooner or later result in reforestation, but during the initial succession stages the abandoned fields are usually covered with grassy vegetation.

## AIMS OF THE STUDY

The present study aimed at obtaining an understanding of the energetical significance of the litter- and soil-inhabiting Annelida and Arthropoda in an abandoned grass field in Central Sweden. These animal groups were chosen since they are some of the most important soil animals of temperate grasslands, and only Protozoa and Nematoda can attain similar importance in certain soils (cf. Macfadyen, 1963; Nielsen, 1967; Stout & Heal, 1967). The primary aims of the study were:

1. to estimate the annual mean abundance, annual mean biomass, and annual respiration of the litter- and soil-inhabiting annelids and arthropods
2. to distinguish between different feeding categories of the annelids and arthropods in order to assess the biomass and respiration of different trophic groups
3. to estimate the net primary production, the plant litter production and the inputs from the above-ground fauna to the soil system in order to relate the animal respiration to these supplies of energy.

The estimates according to aim 1 can be given with greater accuracy when based on small taxonomic units, and it was decided to estimate the abundance, biomass and

respiration for each species, where identification to that level was possible. The species level also provides a sound basis for separating the annelids and arthropods into feeding categories (aim 2), since even closely related species may have different feeding habits. It was also decided to design the study in such a manner that the annual means would be unbiased estimates, and that the standard error (*s.e.*) originating from the sampling procedure could be followed throughout the calculations.

## ENERGY PATHWAYS

The input of energy to the biotic components of the ecosystems is maintained by the photosynthetic autotrophs, which produce organic matter rich in energy by binding solar energy into simple chemical compounds. The chemically bound energy flows from the green plants through a number of organisms, populations and trophic levels. At each trophic level the chemically bound energy is reduced, since all living organisms need energy for their life processes and dissipate the energy as heat. The heat energy losses by respiration are related to other transfers of energy according to the following equations (Petrusewicz & Macfadyen, 1970), which are defined for a given organism, population or trophic level:

$$C = P + R + FU \quad (1)$$

$$A = P + R \quad (2)$$

where:

- $C$ = consumption (ingestion) rate, i.e. the rate of food intake
- $P$ = production rate, i.e. the rate at which food is reorganized into new tissues (including reproductive products)
- $R$ = respiration rate, i.e. the rate at which chemically bound energy within an organism is liberated as heat
- $FU$ = rejection rate, i.e. the rate at which unassimilated food, faeces ($F$), and excretion products ($U$) are delivered
- $A$ = assimilation rate, i.e. the rate at which food is utilized for production and respiration, either by assimilation from the gut (most animals) or by assimilation through the cell wall (microorganisms).

The production rate ($P$) is probably the most composite term of those presented and can be defined as the rate of biomass increase plus the rate of biomass elimination (Petrusewicz & Macfadyen, *op. cit.*).

The transfers of energy given above link together the different organisms in an ecosystem. The main storages and fluxes of energy in a terrestrial ecosystem is exemplified in Fig. 1, where the storages (biomasses, dead organic matter) are indicated by boxes and the fluxes are indicated by arrows. Only above-ground plant parts account for the photosynthesis. Energy fixed in these parts can be translocated to the below-ground parts, but energy may also be translocated in the opposite direction at certain times. Both above- and below-ground parts of the plants provide food for herbivores, but the

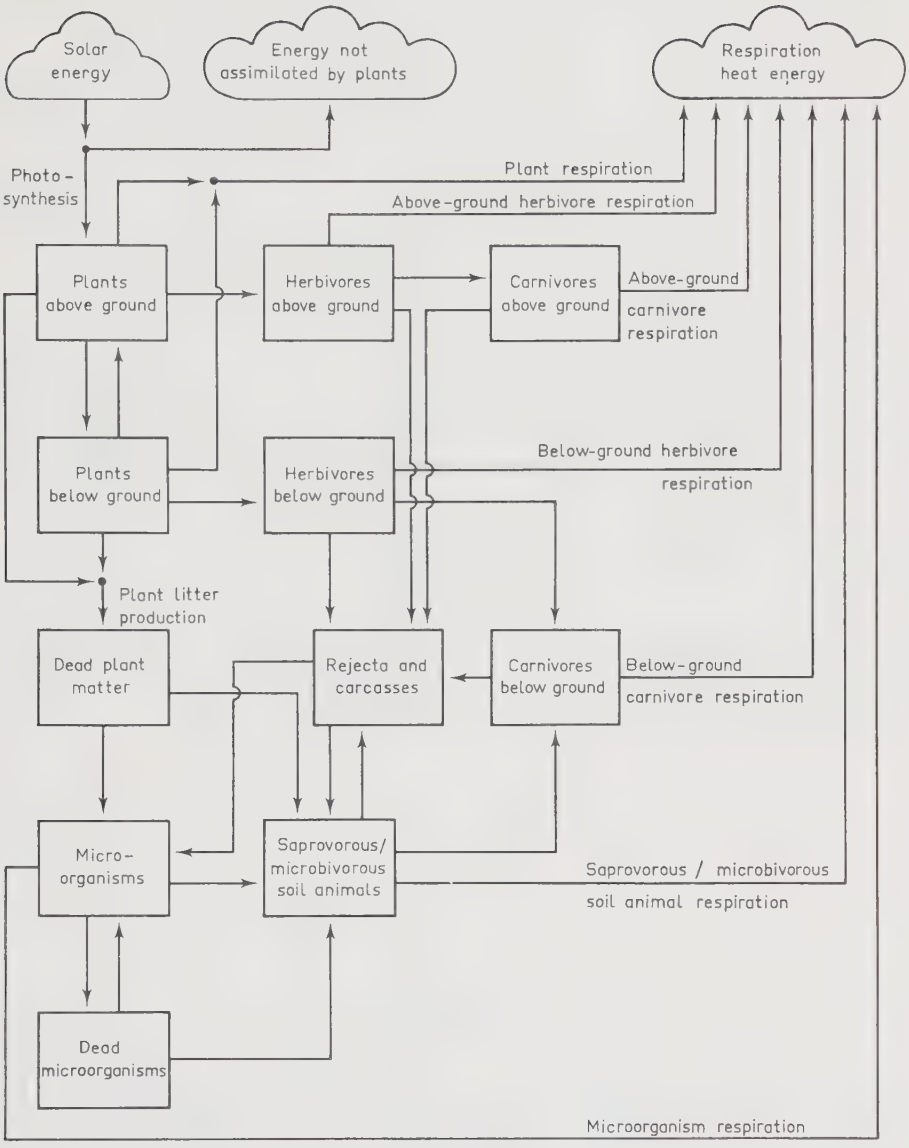


**Figure 1.** Energy flow diagram of a terrestrial ecosystem. Quadrats denote storages of energy, arrows denote transfers of energy and "clouds" denote energy outside the biotic components of the ecosystem. Immigration and emigration are neglected.

amount of energy passing from the living plants to the herbivores is generally of a subordinate magnitude in most terrestrial ecosystems in comparison with that passing from the dead plants to the saprovores (cf. Macfadyen, 1963; Odum, 1971). The dead leaves and stems are deposited on the soil surface, forming a litter layer, while dead roots and rhizomes become below-ground litter. The total production of plant litter constitutes the main input to the stock of dead organic matter. Faeces and carcasses from the herbivores and from the herbivore predators are other inputs to the saprovores.

The dead plant matter is digested by saprovorous microorganisms and animals. The microorganisms are primarily responsible for the chemical decomposition of the dead plant matter, while the soil fauna are mostly restricted to more easily digested substances (Witkamp, 1971). However, some members of the soil fauna are capable of digesting long-chain polysaccharides like cellulose either through the possession of necessary enzymes, or a symbiotic gut flora (Nielsen, 1962; Luxton, 1972). Many soil animals are microbivores (e.g. fungivores and bacterivores), which feed directly on the microorganisms or ingest decaying organic matter from which they assimilate cell contents from the microflora.

Both saprovorous and microbivorous soil animals support populations of soil-dwelling carnivores with food. Since the below-ground carnivores also feed on below-ground herbivores, the carnivores link together the herbivore and saprovore food chains in the soil. Most animals produce faeces, which together with urine excretion products are considered as rejecta in Fig. 1. In most cases the rejecta reach the soil and provide food for saprovorous animals and microorganisms. Dead microorganisms and dead animals (carcasses) are also digested by saprovorous organisms. Rejecta and carcasses are pooled in Fig. 1.

The investigations reported here were mainly performed in 1969–72. The vegetation and some parts of the soil fauna were studied in 1969 and 1970, but the essential and most intensive work was made during the period 15 April 1971 – 14 April 1972. All annual means and annual totals estimated are referred to this period.

# SITE DESCRIPTION

## STUDY AREA

The study area (latitude 60°00′ N, longitude 17°19′ E) is an abandoned field of about 15 ha belonging to the Spikbole farm, 25 km northwest of Uppsala, Sweden (Fig. 2). The field is fairly even and situated 42–44 m above sea level. The upper layer of the soil consists of a loose fen peat soil overlying a subsoil of clay on top of moraine. The moraine reaches the surface at many places outside the field.

**Figure 2.** Geographic situation of the study area, Spikbole, in relation to Uppsala, Stockholm and the IBP site at Andersby ängsbackar.

The area is situated in the southwestern part of a former mire system, Bälinge mossar (Fig. 3), which was drained in 1905–1910 (Eriksson, 1912). The draining enterprise was successful and a great part of the former mire was made arable (Fig. 4). The Spikbole area was used for agriculture from about 1920, mainly as hay land, but barley and oats were also grown. The drainage and cultivations reduced the peat cover and, according to the former owner, the soil surface was lowered by nearly one meter from 1927 to 1967 in some parts of the area. During the 1950s and 1960s the plough reached down to the clay and the underlying moraine to an ever increasing extent. The area was abandoned for agriculture in 1967.

The research plot (Figs. 5 and 6), measuring 50 × 100 m, is oriented in a nearly north-south direction. It is situated on an area last ploughed in 1962 and subsequently used for hay crops until 1967. The upper 15–25 cm of the soil within the plot consists of fen peat soil resting on clay (Fig. 7). Only in the southeastern corner of the plot is the peat layer deeper than 25 cm. In other parts of the plot the peat is mixed with clay as a result of earlier ploughing, but the clay content in the upper 16 cm is usually low, which is shown by the high values of loss on ignition in Table 1. This table also shows the pore volume and the dry bulk density in the upper 40 cm of the soil, excluding the litter layer. The organic content of the litter and upper 40 cm of the soil (excluding roots and rhizomes) was estimated at 41.5 (*s.e.* = 2.8) kg ash-free dw $m^{-2}$ in November 1974. The pH as measured in water was about 5.8 in the peat layer and 6.5 in the clay.

**Table 1. Soil physical data from Spikbole. The values are based on a random sampling (n = 8) in November 1974. Soil cores were dried at +105°C and ignited at +550°C. All estimates are given with 95 % confidence intervals.**

| Depth (cm) | Pore volume (%) | Bulk density (g dry wt $cm^{-3}$) | Loss on ignition (% of dry wt) |
|---|---|---|---|
| 0– 8 | 83.8 ± 2.4 | 0.26 ± 0.06 | 47.5 ± 9.0 |
| 8–16 | 78.7 ± 4.4 | 0.36 ± 0.12 | 47.3 ± 5.0 |
| 16–24 | 70.5 ± 6.9 | 0.64 ± 0.23 | 32.7 ± 15.0 |
| 24–32 | 55.0 ± 7.4 | 1.20 ± 0.23 | 9.5 ± 7.8 |
| 32–40 | 50.8 ± 2.8 | 1.31 ± 0.10 | 3.5 ± 0.7 |

The research plot is surrounded by a 25 m wide buffer strip of open grassland. The major part of the plot is drained by a 1.5 m deep ditch 10–15 m north of the plot (Fig. 5). North of the ditch there is a stand of birch, *Betula pubescens* Ehrh., and spruce, *Picea abies* (L.) Karst. To the southeast of the plot is a stand of spruce with scattered elements of birch and aspen, *Populus tremula* L., on a moraine hillock, and to the southwest there is a 5 m high rocky outcrop with some junipers, *Juniperus communis* L. In all other directions the plot is surrounded by fields.

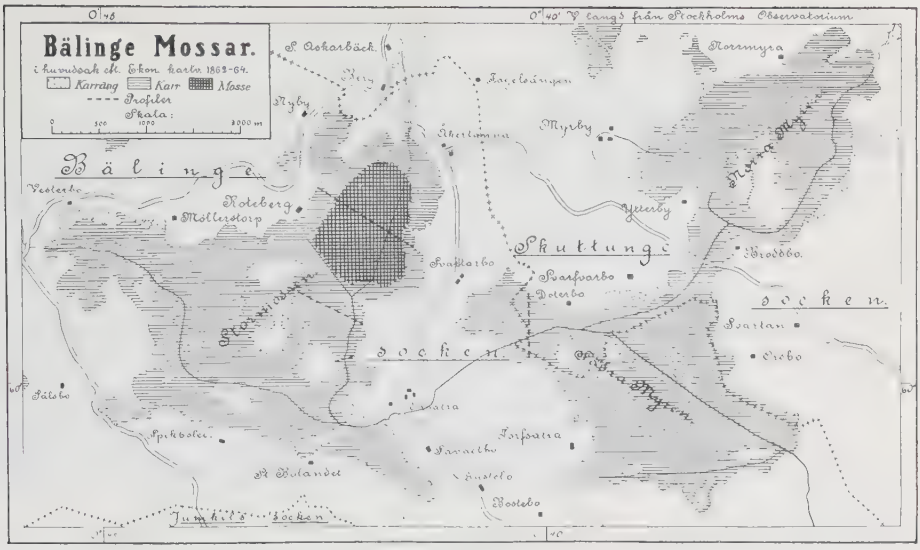


**Figure 3.** Bälinge mossar in 1862–64, more than 40 years before the drainage. The mire system covers 15.9 km$^2$, of which the major part is fenland. Spikbole lies in the southwestern part of the area. Reprinted from Eriksson (1912) by permission of Svensk Botanisk Tidskrift.

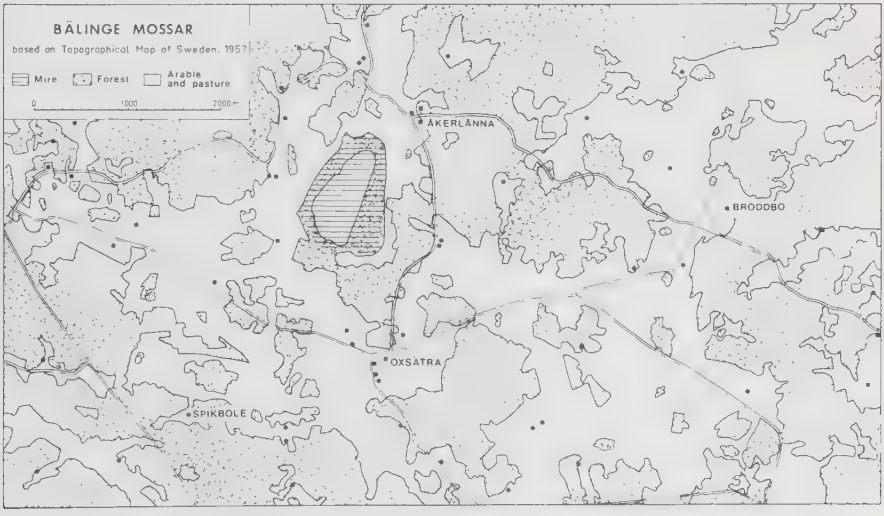


**Figure 4.** Bälinge mossar in 1957, when most of the former mire had been reclaimed and was used for agriculture. The elevated areas are mostly covered with forest. (Permission for distribution approved by the Security Officer, the National Land Survey of Sweden, 1977–03–25.)

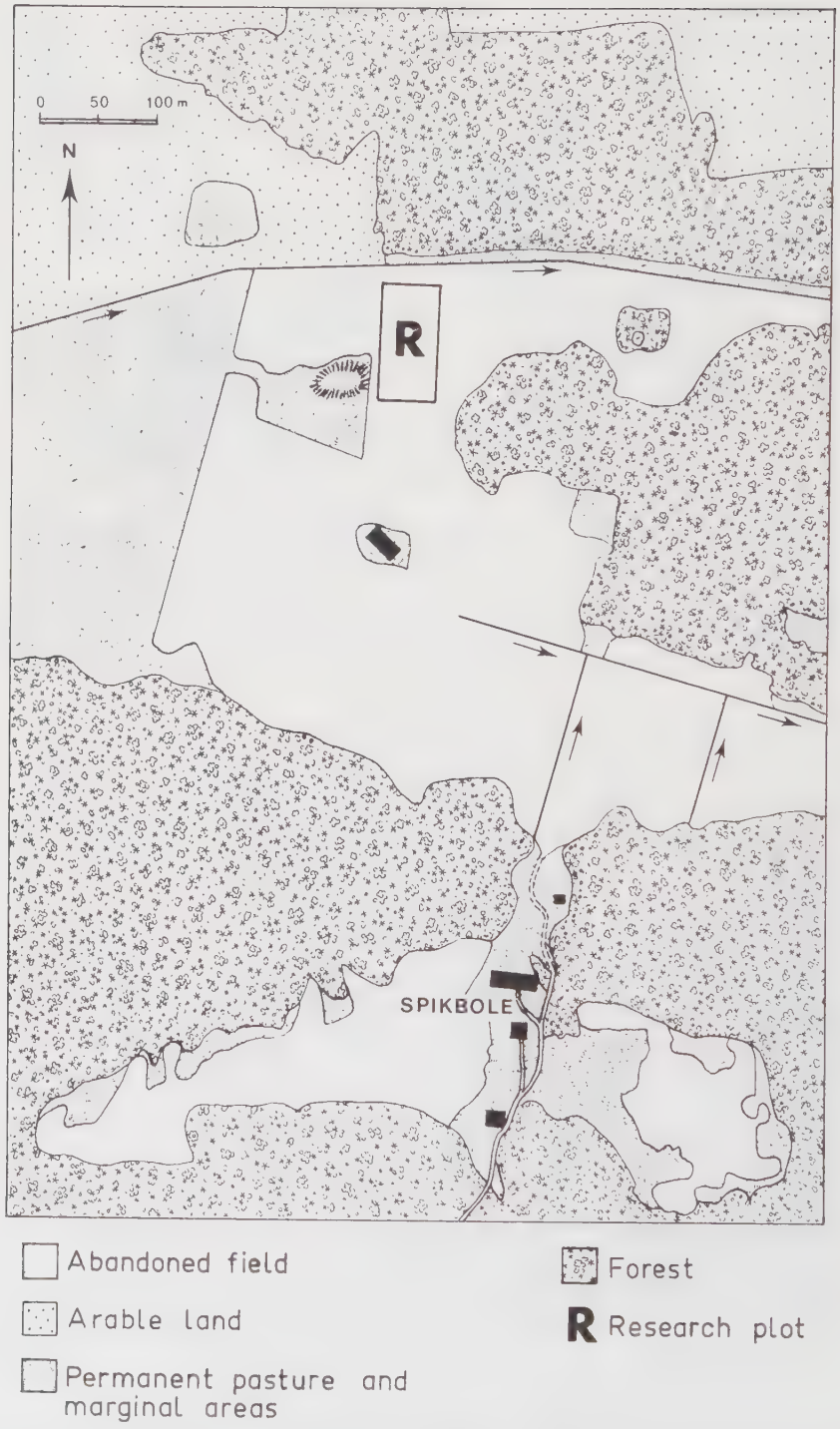


**Figure 5.** The study area and the location of the research plot. (Permission for distribution approved by the Security Officer, the National Land Survey of Sweden, 1977–03–25.)

**Figure 6.** The research plot at Spikbole from the south. The grass sward mainly consists of *Agropyron repens* (L.) Beauv. Photo: T. Persson, June 1974.

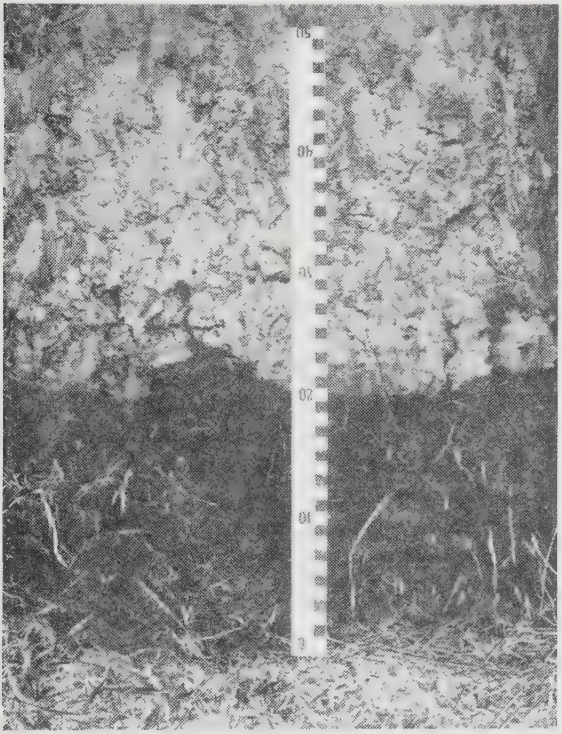

**Figure 7.** Soil profile on the research plot at Spikbole. The upper 20 cm consist of dark peat soil resting on clay. The soil is covered with a 2–5 cm thick litter layer. Photo: T. Persson, May 1973.

In 1969–72 the vegetation on the research plot was dominated by quackgrass, *Agropyron repens* (L.) Beauv., while *Phleum pratense* L., *Festuca pratensis* Huds., *Galium mollugo* L. and *Taraxacum officinale* Weber s.l. occurred more sparsely (cf. Primary producers, p. 26). A bottom layer was almost absent, but some small mosses could be found where the grasses grew thinner. The soil was covered with a litter layer, which was about 2–5 cm thick when undisturbed. No trees or shrubs succeeded in taking root on the plot during 1967–72, but birch and aspen began to invade the margins of the former arable fields in other parts of the area.

## CLIMATE

The Uppsala region lies in an area dominated by westerly and southwesterly cyclones. The cyclones give rise to lively fluctuations between different weather types (Sundborg, 1951). The light and radiation climate of the Uppsala region is determined by the high northern latitude. In June the sun is above the horizon about 18 hours a day and in December 6 hours (Sundborg, *op. cit.*). The real sunshine time per year is about 40 % of the possible with a maximum in June and a minimum in December. Global radiation is about 80 kcal $cm^{-2}$ $yr^{-1}$ (Rodskjer & Tuvesson, 1972). The mean annual air temperature is +5.4°C with a maximum mean monthly temperature of +16.7°C in July and a minimum mean temperature of −5.4°C in February (Table 2). The mean annual precipitation is 518 mm with a marked maximum in the late summer and a minimum in the late winter (Table 3). The growing season, defined as the period when the mean temperature exceeds +3°C, is about 200 days (Ångström, 1958).

## METEOROLOGICAL OBSERVATIONS

Measurements of air temperature, precipitation and global radiation were not performed at Spikbole, and the meteorological data given below come from the meteorological station at the Agricultural College of Sweden, Ultuna, Uppsala. The station is situated 30 km southeast of Spikbole, 20 m above sea level.

Global radiation, i.e. the solar radiation (300–3000 nm) from sun and sky on a horizontal surface, was measured with a Moll-Gorczynski pyranometer. During the period 1969–72 the global radiation was 87.7 (1969), 80.4 (1970), 83.4 (1971) and 77.3 (1972) kcal $cm^{-2}$ $yr^{-1}$. The air temperatures were measured in a standard screen 2 m above ground. The monthly and annual mean temperatures during 1941–70 and for each of the years 1969–72 are given in Table 2. During the main study period 15 April 1971 – 14 April 1972 the mean air temperature was +5.5°C. The monthly and annual precipitation in 1941–70 and for each of the years 1969–72 are shown in Table 3. The annual precipitation was less than normal during the whole period 1969–72. During the main study period 15 April 1971 – 14 April 1972 the precipitation amounted to 429 mm at Ultuna.

Table 2. Monthly and annual mean temperatures (°C) 2 m above ground at the meteorological station, Agricultural College of Sweden, Ultuna, Uppsala.

| | Mean 1941–70 | 1969 | 1970 | 1971 | 1972 |
|---|---|---|---|---|---|
| January | - 5.3 | - 3.9 | - 9.3 | - 1.7 | - 6.0 |
| February | - 5.4 | - 7.7 | -13.3 | - 2.0 | - 2.2 |
| March | - 1.9 | - 5.7 | - 1.7 | - 3.1 | - 0.4 |
| April | + 4.0 | + 3.8 | + 1.8 | + 2.7 | + 3.2 |
| May | + 9.6 | + 9.1 | + 9.9 | +11.5 | + 9.1 |
| June | +14.7 | +16.5 | +17.0 | +14.4 | +16.1 |
| July | +16.7 | +17.6 | +15.3 | +16.9 | +18.9 |
| August | +15.5 | +17.7 | +15.5 | +15.1 | +15.3 |
| September | +11.4 | +11.4 | +10.8 | + 9.6 | +10.1 |
| October | + 6.4 | + 6.9 | + 6.2 | + 6.4 | + 6.1 |
| November | + 1.0 | 0.0 | - 0.6 | - 0.3 | + 2.1 |
| December | - 2.1 | - 6.6 | - 1.8 | 0.0 | + 3.2 |
| Annual mean | + 5.4 | + 4.9 | + 4.2 | + 5.8 | + 6.3 |

Table 3. Monthly and annual precipitation (mm) at the meteorological station, Agricultural College of Sweden, Ultuna, Uppsala.

| | Mean 1941–70 | 1969 | 1970 | 1971 | 1972 |
|---|---|---|---|---|---|
| January | 39.1 | 30.5 | 34.4 | 28.9 | 13.7 |
| February | 26.1 | 24.3 | 9.3 | 33.4 | 30.8 |
| March | 20.9 | 11.0 | 29.5 | 24.8 | 25.6 |
| April | 29.4 | 38.9 | 59.9 | 15.4 | 27.5 |
| May | 33.9 | 36.0 | 4.5 | 13.4 | 29.1 |
| June | 43.9 | 3.0 | 28.9 | 10.9 | 24.9 |
| July | 64.0 | 42.2 | 80.9 | 87.2 | 23.6 |
| August | 69.6 | 67.5 | 14.6 | 86.1 | 74.9 |
| September | 49.0 | 63.4 | 43.1 | 29.5 | 41.0 |
| October | 49.1 | 15.4 | 47.5 | 33.8 | 27.8 |
| November | 49.2 | 69.3 | 62.0 | 47.4 | 38.6 |
| December | 43.9 | 21.1 | 23.6 | 29.5 | 16.6 |
| Annual | 518.0 | 422.6 | 438.2 | 440.3 | 374.1 |

It is well-known that local variations in weather can be considerable even over small distances (cf. Sundborg, 1951). Almquist (1929) stated that the western part of the province of Uppland, to which Spikbole belongs, seems to have lower autumn and winter temperatures than the rest of the province. According to Angström (1958), the duration of the snow cover would be about 110 days in that area while only 100 at Uppsala. Observations during the period 1969–72 confirmed that the snow cover is deeper and melts later at Spikbole than in the surroundings of Uppsala. The meteorological data from Ultuna thus give only rough approximations of the weather at Spikbole.

The main study period 1971–72 started just after the frost had left the soil. The first three months were unusually dry in the province of Uppland, which suffered from drought during June and the beginning of July. The drought was broken by heavy rains in the middle of July, and more rain than normal fell in July and August. The first snow came in November, which had a lower temperature than normal. The snow cover later disappeared and the ground was bare of snow during December and almost the whole of January. Since January was cold the frost could penetrate to a depth of 15–18 cm in the peat soil which was deeper than with normal snow cover. During February the snow cover was about 20–30 cm. A warm spell resulted in the ground becoming almost bare in mid-March, but more snow came during the last week of March. The snow had melted before the end of the main study period on April 14. Some days later the last frost was observed at a depth of 10 cm.

## SOIL TEMPERATURE

The soil temperature was continually recorded by a thermograph (Nr. 256, Wilh. Lambrecht, Göttingen) during the main study period 15 April 1971 – 14 April 1972 at a depth of 5 cm. The daily mean soil temperatures at that depth were calculated as an average of the daily maximum and minimum values. The fluctuations of the daily mean soil temperatures over the main study period are illustrated in Fig. 8.

The main study period was divided into a "summer" period 15 April 1971 – 14 December 1971 consisting of 244 days, and a "winter" period 15 December 1971 – 14 April 1972 consisting of 122 days (cf. General methods, p. 30). The mean soil temperature for the whole "summer" period was +7.6°C. The mean soil temperature for the "winter" period was –0.9°C. The mean soil temperature for the whole annual period was +4.8°C, thus 0.7°C less than the mean air temperature at Ultuna.

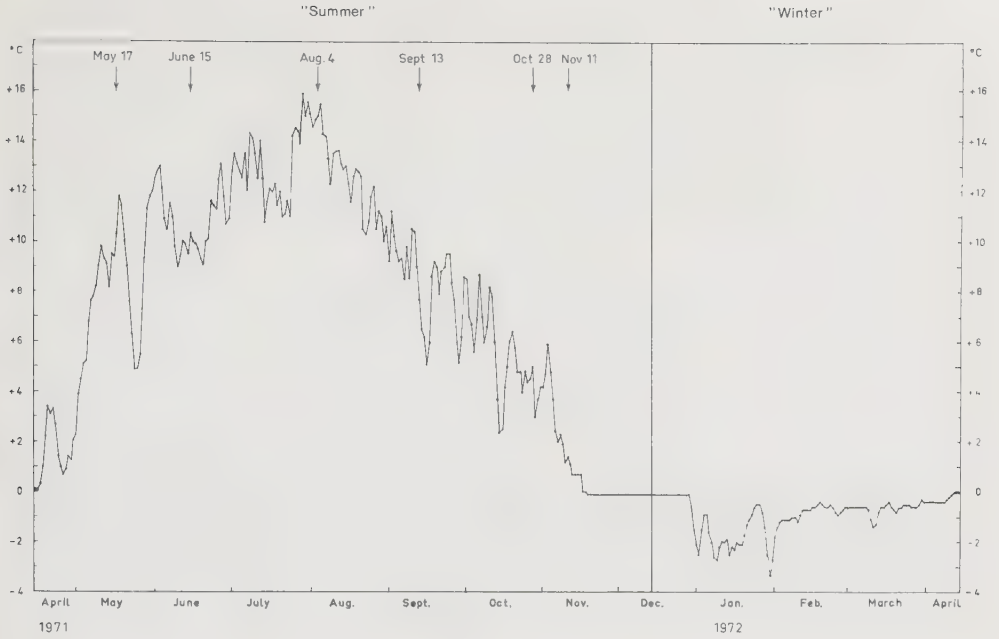


**Figure 8.** Daily mean temperatures at a depth of 5 cm during the study period 15 April 1971 – 14 April 1972. Arrows indicate sampling days during the "summer" period. The daily mean temperatures were +10.3°C (May 17), +10.3°C (June 15), +15.0°C (August 4), +7.7°C (September 13), +5.0°C (October 28) and +1.4°C (November 11). The "winter" mean temperature was -0.9°C.

# PRIMARY PRODUCERS

## INTRODUCTION

The aims of this part of the study were to estimate the net primary production (NPP) and the plant litter production (PLP) during the main study period 1971–72, since the annual NPP constitutes the supply of energy to the herbivores, and the PLP constitutes the main supply of energy to the saprovores. During the study period the primary producers at Spikbole mainly consisted of perennial grasses.

## METHODS

The above-ground vegetation was sampled on June 1, July 7 and August 12 in 1969, and on June 25, July 8 and August 5 in 1970 in order to estimate the peak above-ground biomass for each of the plant species. One sampling was also performed on 4 August 1971. On each occasion quadrats measuring 0.5 × 0.5 m were used as sample units. In June 1969 two primary units measuring 3 × 3 m were chosen at random with the aid of a coordinate grid. Within each primary unit, two 0.25 $m^2$ quadrats were selected at random. This sampling design was only used once, and on July 7 and August 12 of the same year the research plot was divided into four strata of equal size, in each of which two 0.25 $m^2$ quadrats were chosen at random. At each sampling of above-ground biomass in 1970 and 1971 the quadrats were selected according to simple random sampling. All plant shoots, including dead parts attached to the plant, were clipped off a ground level. The shoots were separated into species, taken to the laboratory and were immediately oven-dried at +85°C for 24 hours and weighed to the nearest 0.01 g.

The net production of *Agropyron repens* was estimated by a harvesting method adapted to the characteristics of this species. *A. repens* is a perennial grass with aerial shoots, rhizomes and roots. The aerial shoots start active growth in May, and the spring emergence and early development of new aerial shoots is associated with a net loss of dry material from the old rhizomes (Håkansson, 1967). A dry weight minimum of below-ground parts generally occurs when the primary shoots have reached the 3–4 leaf stage, and after that the dry weight increases, both in the older and the newly formed rhizomes

(Håkansson, 1974). The current year's rhizomes grow actively during the summer until the growth ceases towards the end of September (Palmer, 1958; Hakansson, 1967). The rhizomes may survive for about three years in undisturbed pure stands (Sagar, 1961). The method used here is based on the fact that the current year's rhizomes can be distinguished from the older ones at the end of the growing season.

On 28 October 1971, when the rhizome growth had ceased, a sample of 91 *A. repens* plants (here defined as a unit of connected old and new rhizomes, roots and shoots) were taken at random outside the research plot. Each plant was carefully dug up and cleaned of soil. Dead and alive aerial shoots attached to the rhizomes, and rhizomes and roots formed during the current year were separated from each other, counted, dried at +85°C and weighed. The number of plants $m^{-2}$ in October could be estimated by combining the number of aerial shoots per plant with the number of aerial shoots $m^{-2}$ at the August sampling in the same year. Juvenile primary shoots were omitted from the estimates under the assumption that these shoots would develop into aerial shoots during the next growing season. The method used here presupposes that the older rhizomes are compensated for the losses of soluble organic substances so that the growth increment measured was not dependent on additions from parts produced in a preceding year. Oven-dried samples of aerial shoots, rhizomes and roots were burned in a Gallenkamp adiabatic bomb calorimeter for determination of calorific content. The aerial shoots used for bomb calorimetry were sampled in August and the rhizomes and roots were sampled in October.

## RESULTS

The vegetation at Spikbole was very homogenous in 1969–71. The plant cover was dominated by *A. repens*, which accounted for 80–90 % of the total above-ground biomass on all sampling occasions. The total above-ground biomasses in 1969 were estimated at 107 (*s.e.* = 34), 418 (*s.e.* = 20) and 478 (*s.e.* = 35) g dw $m^{-2}$ on June 1, July 7 and August 12, respectively. The corresponding biomasses in 1970 were estimated at 399 (*s.e.* = 32), 432 (*s.e.* = 20) and 541 (*s.e.* = 45) g dw $m^{-2}$ on June 25, July 8 and August 5, respectively. The peak above-ground biomass thus seemed to occur in the late summer, and the August estimates were considered as being approximate peak values. Few plant species seemed to reach their maximum biomass earlier than the maximum of the whole plant community. The sum of maximum biomasses for all species in 1969 and 1970 was only 2.7 and 1.0 % higher than the corresponding August value, respectively. The above-ground plant biomasses in August 1969–71 are presented in Table 4 and the total values here are considered as peak values.

On average there were 4.64 aerial shoots per *A. repens* plant on 28 October 1971 and, since the mean number of aerial shoots of *A. repens* was estimated at 2719 (*s.e.* = 217) $m^{-2}$ on 4 August 1971, the mean number of plants should be 586 (*s.e.* = 47) $m^{-2}$ both in August and October. The dry weights of the different fractions of *A. repens* could, consequently, be estimated on an areal basis on October 28. The above-ground biomass decreased from 359 (*s.e.* = 31) g dw $m^{-2}$ on August 4 (Table 4) to 236 (*s.e.* = 36) g dw $m^{-2}$ on October 28 (Table 5). The below-ground biomass of the current

Table 4. Above-ground plant biomasses (g dry weight $m^{-2}$) in August 1969–71. + denotes a value less than 0.05.

| | 12 August 1969 | | 5 August 1970 | | 4 August 1971 | |
|---|---|---|---|---|---|---|
| | $\bar{x}$ | s.e. | $\bar{x}$ | s.e. | $\bar{x}$ | s.e. |
| *Phleum pratense* | 32.4 | 10.2 | 20.3 | 11.1 | 9.2 | 4.1 |
| *Deschampsia caespitosa* | 1.5 | 1.5 | 0 | | 0 | |
| *Festuca pratensis* | 4.6 | 3.3 | 12.4 | 8.0 | 0 | |
| *Agropyron repens* | 424.6 | 39.7 | 462.5 | 47.0 | 359.3 | 30.7 |
| *Polygonum convolvulus* | 0 | | 0.6 | 0.4 | 0 | |
| *Chenopodium album* | 0 | | + | | 0 | |
| *Ranunculus auricomus* | 0 | | 0 | | 0.4 | 0.4 |
| *R. acris* | 0 | | 0 | | 0.1 | 0.1 |
| *Erysimum cheiranthoides* | 0 | | + | | 0 | |
| *Vicia cracca* | 0 | | 0 | | 0.9 | 0.9 |
| *Veronica arvensis* | 0 | | 0.1 | 0.1 | + | |
| *Galium mollugo* | 5.6 | 4.3 | 43.7 | 35.0 | 31.2 | 29.1 |
| *Taraxacum officinale* | 8.6 | 4.2 | 1.0 | 0.8 | 6.2 | 3.9 |
| Total | 478 | 35 | 541 | 45 | 407 | 33 |

Table 5. Apparent growth increment of *Agropyron repens* in 1971 according to the sampling on 28 October 1971 (see text).

| | g dry wt $m^{-2}$ | | kcal $g^{-1}$ | kcal $m^{-2}$ | |
|---|---|---|---|---|---|
| | $\bar{x}$ | s.e. | $\bar{x}$ | $\bar{x}$ | s.e. |
| Above-ground shoots | 235.9 | 35.2 | 4.42 | 1043 | 156 |
| Rhizomes (formed in 1971) | 223.1 | 31.4 | 4.20 | 937 | 132 |
| Roots (formed in 1971) | 59.3 | 7.5 | 3.79 | 225 | 29 |
| **Total** | 518.3 | 75.5 | | 2204 | 321 |

year's rhizomes and roots was estimated at 282 (*s.e.* = 41) g dw $m^{-2}$ on October 28. The total dry weight increment of *A. repens* in 1971 up to October 28 was estimated at 518 (*s.e.* = 76) g dw $m^{-2}$. The energy equivalent of this increment was 2204 (*s.e.* = 321) kcal $m^{-2}$ (Table 5).

The above-ground biomass on 4 August 1971 was 48.1 (*s.e.* = 32.2) g dw $m^{-2}$ for plants other than *A. repens* (cf. Table 4). The energy content of *Galium mollugo* L. was estimated at 4.22 kcal $g^{-1}$ at the same time. This value was also used for the other plant species less *A. repens*, and the energy equivalent of their biomass was, consequently, estimated at 203.1 (*s.e.* = 135.8) kcal $m^{-2}$.

## DISCUSSION

The apparent growth increment of about 2200 kcal $m^{-2}$ of *A. repens* was certainly an underestimation of the NPP in 1971, since the consumption by herbivores and losses by death were not included. The reduction of the above-ground biomass from 359 g dw $m^{-2}$ on August 4 to 236 g dw $m^{-2}$ on October 28 can only partly be explained by translocation. Håkansson (1967) estimated the water-soluble carbohydrates to be 23 % of the above-ground dry weight of *A. repens* on July 31. At the most about 25 % of the dry weight (when water-soluble amino acids are also included) could thus have been translocated from the above- to the below-ground parts between August and October. This proportion is equivalent to a translocation of about 90 g dw $m^{-2}$, and the losses by death would thus amount to 34 g dw $m^{-2}$. The latter value was considered to be above-ground litter production between August and October. The NPP excluding herbivore consumption would, consequently be 552 g dw $m^{-2}$ or 2353 kcal $m^{-2}$ for *A. repens* during 1971.

The above-ground biomass of *A. repens* was equivalent to 1590 kcal $m^{-2}$. Thus, the ratio of NPP (excluding herbivore consumption) and the peak above-ground biomass of *A. repens* was 1.48. This ratio was also used for the other plant species less *A. repens*, and their NPP (excluding herbivore consumption) was calculated to be 301 kcal $m^{-2}$ in 1971. The NPP (excluding herbivore consumption) for the total plant community was, hence, 2654 kcal $m^{-2}$ during the same year. The standard error could not be reliably estimated but should be of the order 350 kcal $m^{-2}$.

The consumption by herbivores was indirectly calculated from data on herbivore respiration (cf. Synthesis, p. 177). The above-ground consumption was estimated at 23 kcal $m^{-2}$ during the main study period 15 April 1971 – 14 April 1972, and the below-ground consumption was estimated at 150 kcal $m^{-2}$ during the same period. The total NPP during 1971–72 would, consequently, be 2827 kcal $m^{-2}$ $yr^{-1}$, assuming that the primary production losses owing to respiration between 28 October 1971 and 14 April 1972 were negligible.

The input of plant litter to the soil system was probably dependent on the NPP (excluding herbivore consumption) in 1971 as well as the preceding year's NPP, since the below-ground plant parts were mostly perennial. The annual values of NPP (excluding herbivore consumption) in 1969 and 1970 were calculated in agreement with that in 1971. The annual values for the whole plant community averaged 3112 kcal $m^{-2}$ in 1969 and 3518 kcal $m^{-2}$ in 1970. The mean of the annual values of NPP (excluding herbivore consumption) was 3095 kcal $m^{-2}$ during 1969–71. This was considered as the annual litter production at Spikbole during the main study period 1971–72.

# BELOW-GROUND ANNELIDS AND ARTHROPODS

## GENERAL INTRODUCTION

In a pioneer work Bornebusch (1930) estimated the field respiration of different soil animals by combining population estimates with laboratory determinations of respiration rates. His work provides the first study that emphasized the respiration as a means of assessing the relative importance of soil animals. This approach to the study of the soil fauna has later been used in other investigations (Macfadyen, 1963; Dunger, 1968; Kitazawa, 1971; Huhta & Koskenniemi, 1975, among others). These studies have contributed considerably to the present view of the relative importance of the soil animals for the energy release, although performed at a fairly coarse taxonomic level. More detailed studies of the respiration have been made at the species or life-stage levels but, on the other hand, these studies have been restricted to a limited number of species (O'Connor, 1963; Berthet, 1964; Healey, 1967a, b, among others). The present investigation intended to combine the holistic approach in the studies of community respiration with the more detailed approach in the studies of population respiration in order to obtain thorough knowledge of the below-ground annelids and arthropods. Hence, an attempt was made to estimate the annual respiration of each species belonging to these soil animal groups.

The delimitation between the below-ground fauna (soil fauna) and the above-ground fauna is sometimes hazardous, since many species are not restricted to only one of these habitats. In the present study the below-ground fauna has been defined as "those animals that live on or within the soil either during their whole life or in one or more of their developmental stages. If a species only spends a part of its life in the soil, then only this stage is considered to belong to the below-ground fauna" (cf. van der Drift, 1951). This fairly wide definition implies that true soil dwellers as well as litter- and surface-inhabiting animals are included in the below-ground fauna. Animals that only use the soil for shelter are not included and neither are the inactive stages (eggs, pupae) of insects otherwise classified as above-ground.

The soil fauna has often been classified into different size categories although terminology and delimitation have varied considerably (cf. Murphy, 1953; Dunger, 1964; Ghilarov, 1970). In this study the terms microarthropods and macroarthropods have been used. Only Collembola, Protura, Diplura, Pauropoda and Acari have been considered as microarthropods, while other arthropods occurring at Spikbole were classified as

macroarthropods. Tardigrada, which is an arthropod-like taxon, was neglected in this study.

The most important annelid and arthropod taxa at Spikbole belonging to the below-ground fauna were Enchytraeidae and Lumbricidae (Annelida), and Diplopoda, Collembola, Coleoptera, Hymenoptera, Diptera, Araneae, and Acari (Arthropoda). Other taxa were more sparsely represented and have been treated together in a separate chapter. The most detailed study at Spikbole concerned Collembola and Acari.

During 1969 and 1970 pilot studies were made to gain knowledge of the composition and distribution of dominant annelids and arthropods at Spikbole, and to prepare suitable methods of sample design, extraction technique and treatment of material obtained. The pilot studies mainly concerned Enchytraeidae, Lumbricidae and Collembola, which were assumed to be energetically important taxa in the area. The pilot studies are presented in Appendix 1. The results were used in planning the main study which took place during the period 15 April 1971 – 14 April 1972.

## GENERAL METHODS

### Units for population estimates

Population figures of soil organisms have generally been expressed per unit volume of soil or per unit area of the soil surface. Estimates based on volume units are sometimes disadvantageous, since they must be carefully defined to a given layer or depth not to be misleading when compared with estimates from localities with other soil properties (cf. Macfadyen, 1952). The unit of surface area provides a more unanimous basis and can be more directly used in comparisons. The main reason for choosing the areal unit as a basis was, however, that this study concerned the energy flow through the biotic components of the ecosystem, and both solar radiation, net primary production and litter production are generally given on an areal basis.

### Sampling intensity

The pilot studies (Appendix 1) gave some information of the time expenditure in obtaining a given precision in the estimates. A sample consisting of 15–20 sample units for each type of extraction (see below) should give a standard error of about 10–15 % of the corresponding mean for large taxonomic groups. With that precision the sampling intensity could not exceed six samplings a year without unacceptable cost. The number of samplings could be increased if the number of sample units on each occasion was reduced, but in order not to reduce the precision per sample, it was preferred to perform six samplings with the originally proposed sample sizes.

### Temporal sampling design

The most simple sampling design for estimating the annual means would have been bimonthly samplings during a year. This design was not used, since there is no reliable method of estimating the standard error of the sample mean in a systematic sample

when the statistical population is poorly known (Snedecor & Cochran, 1967:519). Hence, a random sampling design was preferred in order to get unbiased mean values and precision estimates. It was assumed that the period with unfrozen soil would exhibit greater fluctuations in abundance and biomass and higher respiration rates than the period with frozen soil. Therefore, stratified random sampling was used to yield better precision in the estimates. The intensive study period was divided into a "summer" stratum, 15 April 1971 – 14 December 1971, which covered 244 days, and a "winter" stratum, 15 December 1971 – 14 April 1972, which covered 122 days. The boundary between the strata was arbitrarily fixed to a date when the soil was normally getting frozen. The samplings were concentrated to the "summer" period, and five sampling days, May 17, June 15, September 13, October 28 and November 11 were chosen at random from the list of 244 days. A complementary sampling of microarthropods was made on 4 August 1971 in order to obtain information on abundance and biomass during the warmest season. Data from this sampling were not used in calculating the annual estimates.

One sampling was performed during the "winter" period. The positions of the sample units were selected according to a three-dimensional coordinate grid, which had two axes for areal position (see below) and one axis for temporal position. Each sample unit was allotted one day, which was randomly selected from the whole "winter" period. Twenty sample units (for each extraction type) were taken during the "winter". The 20 sampling days could be divided into seven groups, each with a maximum range of seven days, but for practical reasons only one sampling per group was carried out. The allotted dates were thus moved a maximum of 3–4 days, which was assumed to be negligible with regard to changes in abundance and biomass. The "new" sampling days became: December 16, January 10, January 26, February 22, March 7, March 21 and April 5. In the statistical treatment the "winter" sampling was considered to be totally randomized in time with 20 sample units in spite of the reduced number of sampling days.

## Areal sampling design

During the "summer" period each sample usually consisted on 15 sample units per extraction type, whose locations in the field were selected at random from a coordinate system with 0.5 m grid meshes. The five "summer" samplings revealed that the quantitatively most important lumbricid, *Allolobophora rosea* (Sav.), was almost absent in the southwestern part of the research plot, and had relatively high densities in the northeastern part. The uneven distribution caused fairly high standard errors when simple random sampling was performed. Before the "winter" sampling the plot was, therefore, divided into two strata, the southwestern stratum measuring 2800 $m^2$ and the northeastern 2200 $m^2$. The number of sample units per stratum was taken in proportion to the size of the stratum and the estimated standard deviation in order to get optimum allocation with regard to *A. rosea* (Snedecor & Cochran, 1967:523). Seven units were taken from the larger southwestern stratum, and thirteen from the smaller, but more variable, northeastern stratum.

## Sample units

Different sample units were used for collection of microarthropods, macroarthropods, enchytraeids and lumbricids. The sample units were somewhat modified from the "summer" to the "winter" samplings in order to compensate for the vertical migration of some animals. The units intended for collecting micro- and macroarthropods and enchytraeids were taken with cylindrical corers, while the unit used for lumbricid sampling was dug out with spades. The four different soil cores were taken in parallel at each selected sampling location in the research plot. The number of macroarthropod cores was, however, less than the others during the "summer" which is shown in Table 6, which also shows the dimensions of the sample units. The proportions of the sample units and the corresponding sampling devices in relation to the soil profile at Spikbole are illustrated in Fig. 9.

Table 6. Soil fauna samplings in 1971–72. The depths are measured from the litter/soil interface. S denotes stratified random sampling and C denotes the complementary sampling in August not used for estimating "summer" and annual means.

| | May 17 1971 | June 15 1971 | Aug 4 1971 (C) | Sept 13 1971 | Oct 28 1971 | Nov 11 1971 | Dec 15–Apr 14 1971–72 |
|---|---|---|---|---|---|---|---|
| **Microarthropod sampling** | | | | | | | |
| Surface area ($cm^2$) | 10.8 | 10.8 | 10.8 | 10.8 | 10.8 | 10.8 | 10.8 |
| Depth (cm) | 20 | 20 | 20 | 20 | 20 | 20 | 26 |
| Sample size (n) | 15 | 15 | 15 | 15 | 15 | 15 | 20 (S) |
| **Macroarthropod sampling** | | | | | | | |
| Surface area ($cm^2$) | – | 188 | – | 188 | 188 | 188 | 188 |
| Depth (cm) | – | 3 | – | 3 | 3 | 3 | 3 |
| Sample size (n) | – | 10 | – | 10 | 10 | 10 | 20 (S) |
| **Enchytraeid sampling** | | | | | | | |
| Surface area ($cm^2$) | 22.1 | 22.1 | – | 22.1 | 22.1 | 22.1 | 22.1 |
| Depth (cm) | 20 | 20 | – | 20 | 20 | 20 | 28 |
| Sample size (n) | 15 | 15 | – | 15 | 15 | 15 | 20 (S) |
| **Lumbricid sampling** | | | | | | | |
| Surface area ($cm^2$) | 625 | 625 | – | 625 | 625 | 625 | 625 |
| Depth (cm) | 30 | 30 | – | 30 | 30 | 30 | 60 |
| Sample size (n) | 15 | 15 | – | 15 | 15 | 15 | 20 (S) |

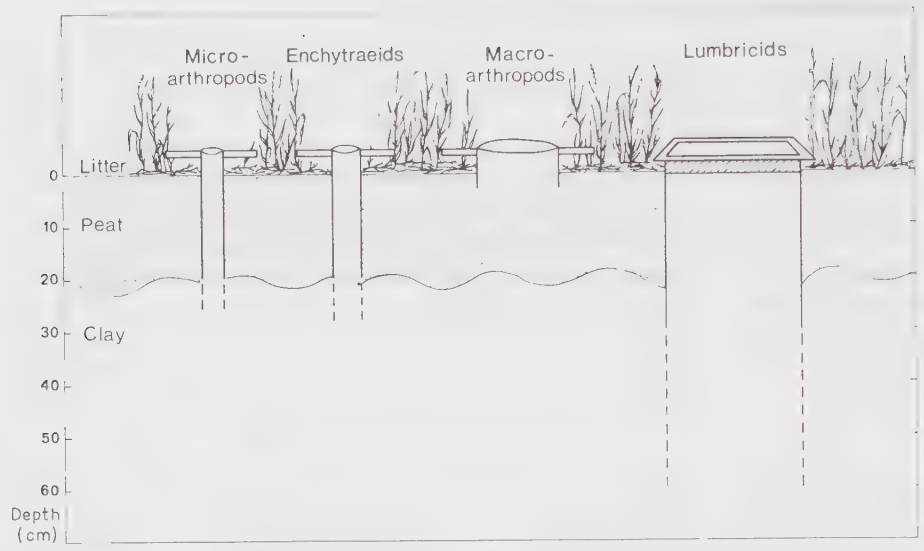


**Figure 9.** Soil cores and corresponding sample devices used in estimating different soil fauna groups. The broken lines indicate the increased sample depths during the winter period 1971–72.

## Microarthropod sample treatment

The microarthropod sampler removed soil cores with 10.8 $cm^2$ surface area and 20 cm depth during the "summer" period. The great porosity of the soil resulted in the cores being compressed to about 16 cm. During the "winter" the cores were taken to a depth of 26 cm. Because of the frost the soil structure was retained during the "winter". The sampler could not always be forced through the frozen soil, and sometimes it was necessary to carve out soil monoliths to fit the corer. The sampler consisted of a split corer in which 2 cm high rings of hard pasteboard were inserted. Each soil core was removed from the corer enclosed in the rings and was taken to the laboratory in a polythene bag. While still remaining in the rings the soil cores were divided into 2 cm slices, which were placed in extractors of Macfayden's high gradient canister type (Macfadyen, 1961), further developed at the Mols laboratory in Denmark (Petersen, in prep.). Each of the soil slices was inverted over a metal gauze (1.0 × 1.5 mm mesh size) on top of a canister with picric acid solution as collecting fluid. A temperature gradient was maintained throughout the soil slices by heating from above with electric light bulbs and cooling the collecting jars from below. The collecting jars were immersed in a water bath, which was cooled to about 0–2°C by refrigerator coils. The temperature gradient was increased each day by means of a transformer, which controlled the voltage. The temperature was increased up to +42°C in the top and +30°C in the bottom of the sub-core after four days of extraction. The temperature gradient throughout the extraction time is shown in Fig. 10. After extraction, 99 % ethanol was added to the picric acid solution to get a more isotonic fluid, which neither shrinked nor expanded the extracted animals.

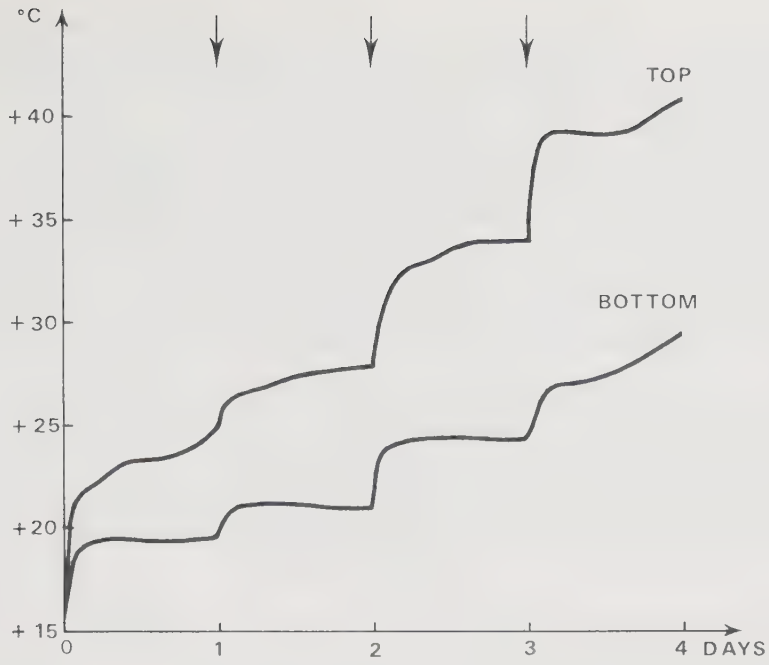


**Figure 10.** Temperature changes during the extraction of a 2 cm thick peat soil core in a Macfadyen high gradient canister extractor. Arrows indicate increased light intensity.

The high gradient canister apparatus is an extractor based on the Tullgren funnel principle, but with additional arrangements for maintaining steep temperature and humidity gradients in the soil core. The animals fall directly into the conservation fluid, which is an advantage over the funnels, since soft-bodied animals may adhere to the sloping walls. The extraction is considered to yield two to ten times as many animals as a standard Tullgren-type funnel (Macfadyen, 1961). According to a test by Edwards & Fletcher (1971) the efficiency of the high gradient canister extractor was sometimes lower than that of some other modern extractors, but their results are not relevant to the present study since they used a widely different temperature regime. In accordance with Block's (1966b) description they obtained as high as +120°C in the top and +50°C in the bottom layer of the soil core after three days of extraction. The high gradient canister extractor has also been tested by Marshall (1972), who increased the temperature up to +38°C at the top and +35–37°C at the bottom of the soil core. He recovered about 80 % of the number of Collembola and 85–89 % of the number of Acari which had been introduced into defaunated soil cores.

## Macroarthropod sample treatment

The small surface area of the microarthropod soil cores meant that large collembolans and other large-sized arthropods, usually not very abundant, were estimated with a fairly low degree of precision. Most of these arthropods were found in the litter layer and

it was decided to take cores measuring 188 $cm^2$ from the litter and the top-soil layer to a depth of 3 cm. These macroarthropod sample units were first used on 15 June 1971, since it was not realized earlier that the microarthropod sampler yielded estimates with low precision for larger arthropods.

The above-ground vegetation was included in the sample unit, as well as the snow covering the position of the selected core during the winter. The snow was separated from the litter and soil in the field. The soil and snow cores were taken to the laboratory in polythene bags. The snow was melted and searched for animals. The soil cores were placed in large Tullgren funnels (25 cm in diameter) on a wire gauze sieve and extracted for four days. The heat was obtained from a 40 W electric bulb placed about 25 cm above each funnel. The extracted animals were collected in jars containing 80 % ethanol.

The efficiency of the Tullgren funnels was assumed to be low with regard to small and slightly sclerotized arthropods, but acceptable for mobile and larger species. This assumption was partly confirmed since delicate Nematocera larvae belonging to Cecidomyiidae and Sciaridae, as well as immature Cryptostigmata were sometimes found fastened to the funnel walls, while surface-living Collembola, Gamasina and Coleoptera (both adults and juveniles) were never found on the walls.

### Enchytraeid sample treatment

The enchytraeid sampler removed cores with 22.1 $cm^2$ surface area and 20 cm depth during the "summer" period. During the "winter" the depth was 28 cm. The soil cores were divided into 4 cm long sub-cores, which were put into individual polythene bags in the field before transport to the laboratory. Some of the cores had to be stored for one or two days at +5°C. Before extraction the sub-cores were divided into 2 cm thick slices which were spread on wire gauze sieves resting in water-filled funnels belonging to the extraction apparatus.

The enchytraeids were extracted according to a modified Baermann funnel method described by O'Connor (1955, 1962). The extraction procedure closely followed the description given by O'Connor (1962), and the heating was adjusted to obtain the same temperature gradient. One extraction lasted for three hours. After extraction, the live enchytraeids were counted in a water-filled petri dish and removed to a droplet of water. The water was evaporated and after drying for 24 hours at +60°C in a vacuum-drier the enchytraeids from each soil core were weighed to the nearest 0.01 mg.

The modified Baermann funnel method and a method devised by Nielsen (1952–53) are the methods most commonly used for extracting enchytraeids. Their relative efficiencies have been compared on different soil types by O'Connor (1955, 1962) and Peachey (1962). The difference between the methods was small on mineral soils, but the wet-funnel method was more efficient for extracting enchytraeids from peat soils (Peachey, *op. cit.*). It was therefore decided to use the wet-funnel method in this study. The efficiency of the modified Baermann funnel method has been investigated by Abrahamsen (1972), who recovered 87 % of more than 3000 enchytraeids introduced to defaunated soil cores. However, Abrahamsen (*op. cit.*) concluded that a considerable loss of animals was probably due to the transferring the animals to the cores and, hence, the extraction efficiency should be very high.

## Lumbricid sample treatment

Lumbricids and other large soil invertebrates, e.g. Carabidae, Elateridae, Curculionidae and some Diptera larvae, were sampled by means of taking soil cores measuring 625 $cm^2$ in surface area to a depth of 30 cm during the "summer" period and down to 60 cm during the "winter". The cores, which included vegetation and the litter layer, were dug out with flat spades. The uppermost soil was cut out with a 25 × 25 cm metal frame with sharpened edges. The soil cores were divided into a 0–10 cm deep layer and a 10–30 cm deep layer before they were transported to the laboratory in polythene bags. During the "winter" the soil was divided into more layers (cf. Lumbricidae). The cores were sorted by hand in the laboratory. The hand sorters were told to search carefully for all animals, also small ones, in order to increase the sorting efficiency. Some soil cores had to be stored for four days at +5°C before they were sorted.

The hand sorting efficiency was probably high for large lumbricids and the largest and most mobile arthropods, for example some Carabidae, and for white Curculionidae larvae contrasting against the dark soil. Many other arthropods were probably underestimated, and estimates based on hand sorting were only used when other data were inaccurate.

## Weight determinations

After separation from the soil the animals were identified and counted. The individual weights were determined in several ways depending on the size of the animals. The body weights of Lumbricidae, Diplopoda, most Coleoptera, Diptera larvae and Araneae were determined on a Sartorius 2444 balance to the nearest 0.01 mg for each individual. Enchytraeidae, small Diptera and Coleoptera larvae, some other insects and larger Acari were too small to be weighed individually, but were weighed collectively from each soil core.

Smaller species had to be treated in other ways. Individual weights of most Collembola and Acari were determined by length/weight or length/width/weight regressions. Species with moderate variations in body weight, for example adults of Mesostigmata and Cryptostigmata, were weighed in large numbers in order to obtain mean body weights for the whole sampling period. Other specimens were given weights according to the literature. The different methods of determining the body weights are outlined more closely in the presentation of the soil fauna groups.

It may be noticed that the direct weighings of the arthropods were made on animals mostly preserved in 80 % ethanol for one to twelve months. The weights and biomasses obtained in this manner are probably inflicted with errors (cf. Breymeyer, 1967), but no corrections for possible weight losses were made.

## Calculation of respiration

The calculation of field respiration was based on a combination of laboratory measurements and population estimates. The respiration rates of soil animals are generally estimated by measuring the oxygen consumption rates or the carbon dioxide output rates. Rates of oxygen consumption or carbon dioxide evolution were taken or derived from literature references and were, thus, not measured originally in the present study.

The respiration rates have usually been measured at constant temperatures with more or less acclimatized animals classified with regard to species, age, sex and weight. Most investigators ignore respiration occurring during the initial period of enhanced activity caused by the change of environment. There is a considerable difference between respiration rates of resting and moving animals, which has been shown by Zinkler (1966), Miyashita (1969) and Standen (1973) among others. The values used in this study are, if not otherwise stated, based on resting or slowly moving animals.

The heat production per litre oxygen consumed varies somewhat with the type of food substance combusted, e.g. 5.14 kcal for glycogen, 5.08 kcal for sucrose, 5.06 kcal for starch, 4.4–4.6 kcal for fat (Brody, 1945) and 4.3–4.7 kcal for protein (Heilbrunn, 1945). The energy release may, thus, differ in relation to oxygen consumption depending on the foodstuffs being used, which in turn usually depends on whether the animal is fasting or not. The presence of possible variations was neglected in this study, and the value for heat production was assumed to be 4.8 kcal per litre $O_2$ (Brody, 1945) for all animals and all sampling occasions. The value used corresponds to a respiratory quotient of about 0.8.

It has long been recognized that a general relationship exists between body size and metabolic rate for specific groups of organisms (Reichle, 1971). The relationship can be described by the power function equation:

$$Q = a \cdot W^b \tag{3}$$

where $Q$ is the oxygen consumption rate of an animal of live body weight $W$, and where $a$ and $b$ are constants. The equation may also be expressed in the form:

$$\frac{Q}{W} = a \cdot W^{b-1} \tag{4}$$

where $Q/W$ is the oxygen consumption rate per unit weight. The exponent $b$ is usually about 0.7–0.8 for poikilotherms (Zeuthen, 1953; Hemmingsen, 1960), but may range from about 0.5 to 1.0 depending on the type of organism. If $b = 0.67$, the oxygen consumption rate follows the "surface law", i.e. the heat loss is proportional to the body surface, and if $b = 1.0$ the oxygen consumption rate is proportional to weight (Bertalanffy, 1957).

When the exponent $b$ is less than 1.0 the oxygen consumption rate per unit weight increases with decreasing body weight. Since, then, the oxygen consumption rate per unit weight varies with body size, the rates should be calculated for different size classes. The calculation of a rate based on an average animal would give serious overstimations of the true rate, at least for species with a wide range of body weights and a low $b$ value. The constants $a$ and $b$ were sometimes given in the original papers, but often they had to be calculated from the primary data according to the method of least squares.

In most invertebrates the respiratory rate (per individual or per unit weight) rises slowly at low temperatures, then steeply, then slowly to a maximum and then declines sharply as lethal temperatures are approached. At low and mid-range temperatures the

respiratory activity sometimes increases exponentially with temperature according to a constant $Q_{10}$ relationship. The $Q_{10}$ value is, however, seldom constant over a wide range of temperatures, and often the $Q_{10}$ decreases with rising temperature (e.g. Wigglesworth, 1965; Byzova, 1973; Keister & Buck, 1974). An alternative relation between respiratory rate and temperature is given by Krogh's (1941) curve, which is fitted to empirically found respiration rates of different animals. The Krogh curve conforms to the general relationship of higher $Q_{10}$ values at lower temperatures and lower $Q_{10}$ values at higher temperatures. However, the relations between respiratory rate and temperature are generally expressed in terms of $Q_{10}$ values in the literature, and since these relations may deviate pronouncedly from the Krogh curve it was preferred to use exponential or linear relationship with varying $Q_{10}$ values in order to obtain the most accurate temperature correction. The reasons for using a certain $Q_{10}$ are given for each group of organisms. When an exponential $Q_{10}$ relationship was assumed, the rates were corrected according to the formula:

$$Q_T = Q \cdot q^{(T-T_0)/10} \tag{5}$$

where $Q_T$ denotes the oxygen consumption rate at temperature $T$, $Q$ denotes the oxygen consumption rate at temperature $T_0$, i.e. the temperature used in the respirometer or given in a literature reference, and $q$ denotes the $Q_{10}$ value. Since $Q$ is equivalent to $a \cdot W^b$ according to equation 3, the field respiration of a species population can be calculated as:

$$Q_N = a \cdot q^{(T-T_0)/10} \sum_i N_i \cdot W_i^b \tag{6}$$

where $Q_N$ denotes the total oxygen consumption rate of a species with $N$ individuals, $N_i$ denotes the number of animals in the weight class $i$ and $W_i$ denotes the mean live body weight in that weight class.

The $Q_{10}$ value ($q$) was, where necessary, calculated according to the equation:

$$q = \left( \frac{Q_1}{Q_2} \right)^{10/(T_1-T_2)} \tag{7}$$

where $Q_1$ and $Q_2$ denote the oxygen consumption rates at the temperatures $T_1$ and $T_2$, respectively. The calculation presupposes an exponential relationship.

The temperature corrections were made to the field temperature measured at a depth of 5 cm in the soil. The temperatures in other layers certainly differed from those at the 5 cm level but, when considering the vertical distribution of the animals, this depth was assumed to give an approximate mean temperature of the soil animal environment.

The mean soil temperature of each sampling day was used to calculate respiratory rates during the "summer" period. During the "winter" the mean soil temperature for the whole period was used. It should be noted that the daily respiration may be underestimated if the arithmetic mean temperature is used in cases when the respiratory rates are exponentially dependent on the temperature (Solhoy & Skartveit, 1975), but since

the temperature variation within the day was not very great on any of the sampling occasions, this error was neglected.

## Data treatment

The primary aim of the present study was to estimate the annual mean values of abundance and biomass of different soil animals and their annual respiration. The study also intended to estimate the standard error of each mean in order to get an idea of the precision of the estimates. These intentions governed the choice of sampling design which, to our knowledge, has not earlier been applied to soil fauna populations. The mean values ($\bar{x}$) and standard errors (*s.e.*) at each sampling during the summer period were estimated as:

$$\bar{x} = \frac{1}{n} \sum_{i=1}^{n} x_i \tag{8}$$

and

$$s_{\bar{x}} = \sqrt{\frac{\sum_{i=1}^{n} (x_i - \bar{x})^2}{n(n-1)}} \tag{9}$$

where $s_{\bar{x}}$ is the standard deviation of the mean (= standard error), $x_i$ is the value obtained in each individual sample unit, i.e. the number or weight of animals per soil core, or the calculated respiration rate per day per soil core, and $n$ is the number of sample units.

The means of the "summer" period and the corresponding standard errors of abundance, biomass and respiration rates per day were estimated as:

$$\bar{x}_S = \frac{1}{m} \sum_{j=1}^{m} \bar{x}_j \tag{10}$$

and

$$s_{\bar{x}_S} = \sqrt{\frac{\sum_{j=1}^{m} (\bar{x}_j - \bar{x}_S)^2}{m(m-1)}} \tag{11}$$

where S denotes the "summer" stratum, $\bar{x}_j$ is the mean value of each "summer" sampling, and $m$ is the number of "summer" samplings.

Stratified random sampling on an areal basis was used during the "winter" period. The mean values and standard errors were estimated according to:

$$\bar{x}_W = P_A \cdot \bar{x}_A + P_B \cdot \bar{x}_B \tag{12}$$

and

$$s_{\bar{x}_W} = \sqrt{P_A{}^2 \cdot \frac{s_A{}^2}{n_A} + P_B{}^2 \cdot \frac{s_B{}^2}{n_B}} \qquad (13)$$

where W denotes the "winter" stratum, $P_A$ and $P_B$ denote the proportions of strata A and B in relation to the size of the research plot, i.e. 0.44 and 0.56 respectively, $\bar{x}_A$ and $\bar{x}_B$ denote the mean values for strata A and B calculated according to equation 8, and $s_A{}^2$ and $s_B{}^2$ denote the variances of strata A and B. The values of $n_A$ and $n_B$ were 13 and 7, respectively.

The annual means ($\bar{\bar{x}}$) and standard errors ($s_{\bar{\bar{x}}}$) were estimated as:

$$\bar{\bar{x}} = \frac{N_S \cdot \bar{x}_S + N_W \cdot \bar{x}_W}{N_S + N_W} \qquad (14)$$

and

$$s_{\bar{\bar{x}}} = \sqrt{\left(\frac{N_S}{N_S + N_W}\right)^2 \cdot s_{\bar{x}_S}{}^2 + \left(\frac{N_W}{N_S + N_W}\right)^2 \cdot s_{\bar{x}_W}{}^2} \qquad (15)$$

where $N_S$ and $N_W$ denote the numbers of days during the "summer" (244 days) and "winter" (122 days) periods, respectively. The annual respiration of different soil animals was estimated as 366 times the obtained value of $\bar{\bar{x}}$.

The random errors introduced by length/weight regressions or regressions for calculating respiratory rates were neglected. Consequently, the standard errors attached to the final estimates only originated from the sampling procedure as indicated by equations 8–15. The standard errors were generally rounded off upwards. A standard error of 11.1 was thus rounded off to 12 in order not to underestimate the imprecision. However, when the standard error was equal to the mean value, they were both rounded off in the usual manner.

## Background

The Enchytraeidae is a widely distributed oligochaete family, which is most abundant in acidic organic soils and is dependent on a high moisture status (O'Connor, 1971). The abundances are generally found within the range 1000–100 000 $m^{-2}$ (e.g. Nielsen, 1955a), but annual mean abundances of 100 000–200 000 $m^{-2}$ (O'Connor, 1957; Peachey, 1963) and peak numbers of nearly 300 000 $m^{-2}$ have been estimated (Peachey, *op. cit.*). The biomasses often range within 0.3 and 30 g fw $m^{-2}$, although both higher (e.g. Peachey, *op. cit.*) and lower values have been reported.

## Methods

The enchytraeids from each soil core were vacuum-dried at +60°C and weighed collectively to the nearest 0.01 mg. No correction was made for gut content. The live weight was calculated as 5.56 times the dry weight according to Edwards (1967). Species determinations were made on material not used for biomass estimates.

Oxygen consumption rates per unit weight were calculated from Nielsen's (1961) figures on individual *Fridericia* spp., *Henlea perpusilla* Friend and *H. ventriculosa* (Udekem) obtained with Cartesian diver technique at +20°C. A regression equation of the form $Q/W = a \cdot W^{b-1}$, where $Q/W$ denotes $mm^3$ $O_2$ $g^{-1}$ $h^{-1}$, and $W$ denotes g live body weight, was fitted to the values ($n$ = 72) by means of the method of least squares. The equation was found to be $Q/W = 33.6 \cdot W^{-0.33}$. The enchytraeids used by Nielsen for respiration measurements were small or medium-sized. O'Connor (1967) has presented data on large (8–15 mg) *Fridericia ratzeli* (Eisen) and *F. galba* (Hoffm.), and when these values ($n$ = 10) were added to Nielsen's data the new regression equation did not differ from that presented above. The individual values given by Nielsen (*op. cit.*) and O'Connor (*op. cit.*) and the regression line are shown in Fig. 11.

The respiratory rates at field temperatures of +5°C and higher were calculated from the temperature correction curve given by O'Connor (1971). At temperatures below +5°C the respiratory rates were assumed to decrease linearly with the temperature to a zero-value at −5°C, which is in agreement with the temperature correction curve for *Cognettia sphagnetorum* (Vejd.) used by Standen (1973).

## Results

### Species composition

Eight enchytraeid species were identified at Spikbole, namely *Henlea perpusilla*, *H. ventriculosa*, *Fridericia bulboides* N. & C., *F. paroniana* Issel, *F. bisetosa* (Lev.), *F. ratzeli*, *Enchytraeus minutus* N. & C. and *Marionina argentea* (Mich.). The nomenclature follows Nielsen & Christensen (1959, 1961, 1963). The relative abundance of the species could not be recorded owing to the great number of juveniles, some of which were impossible to determine to the species level. However, there was no doubt that *H. perpusilla* was the most abundant species and accounted for about 50 % of the total

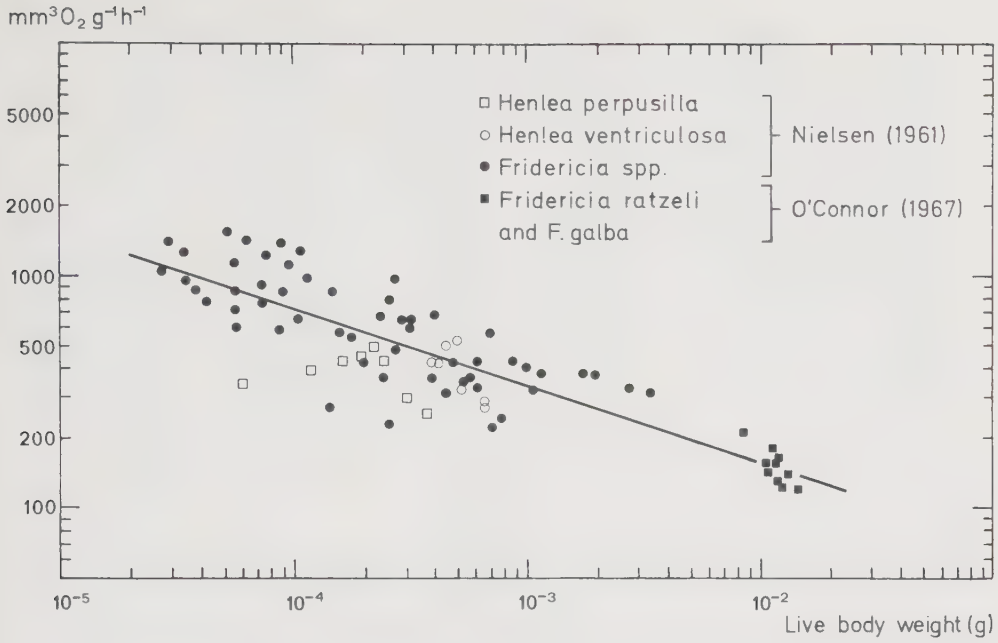


**Figure 11.** Oxygen consumption rates per unit weight of different-sized enchytraeids at +20°C. The regression line is based on Nielsen's (1961) values on individual *Henlea perpusilla, H. ventriculosa* and *Fridericia* spp. O'Connor's (1967) values on large-sized *Fridericia* are given for comparison.

number of enchytraeids. *F. ratzeli* was more sparse, but its large body size implied a contribution in the region of 70 % to the total enchytraeid biomass.

### Vertical distribution

The vertical distribution of Enchytraeidae is illustrated in Fig. 12, which shows that the enchytraeids were always found down to 20 cm. The percentage of enchytraeids extracted from the top 12 cm of the soil profile were 64 in May, 87 in June, 73 in September, 75 in October and 68 in November. The high proportion of enchytraeids in the 16–20 cm level in May was mainly due to the high densities of *Marionina argentea* in some soil cores. During the "winter" 49 % occurred in the top 12 cm, 41 % in the 12–20 cm level and 10 % between 20–28 cm. Some enchytraeids evidently occurred at greater depths during the winter, since one individual of *Fridericia ratzeli* was found by hand sorting at a depth of 40–50 cm in an earthworm tunnel.

### Abundance

The abundance of Enchytraeidae fluctuated within the range 18 000–35 000 $m^{-2}$ with a peak number in May and a low in September (Table 7). The annual mean abundance was estimated at 24 000 (*s.e.* = 2100) $m^{-2}$.

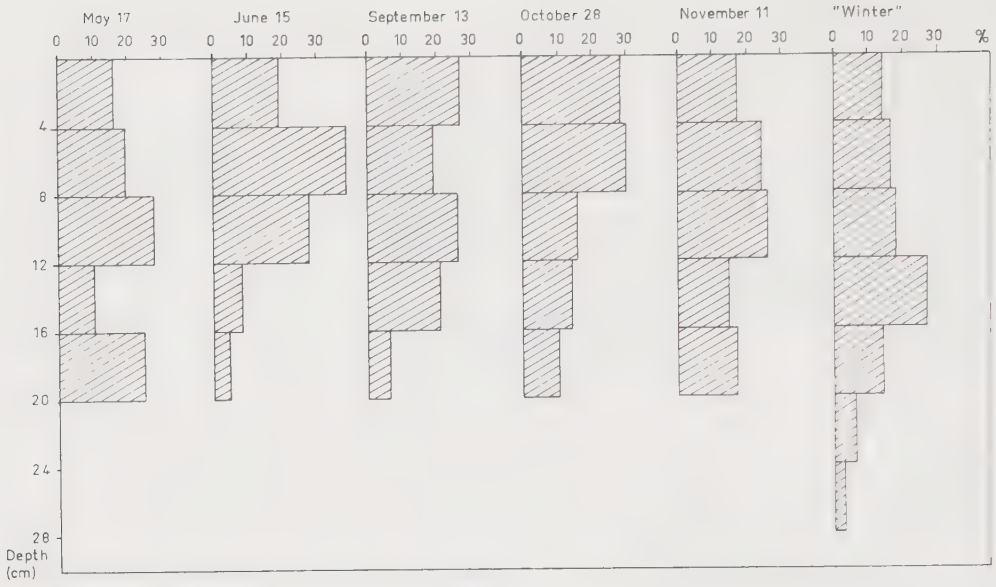


**Figure 12.** The vertical distribution of Enchytraeidae in 1971–72. The numbers of enchytraeids are expressed as percentages of the total number on each sampling occasion.

### Biomass

The biomass ranged from about 0.5 g dw $m^{-2}$ in September to 1.1 g dw $m^{-2}$ in October (Table 7). The annual mean biomass was estimated at 0.85 (*s.e.* = 0.09) g dw $m^{-2}$, which corresponds to a biomass of 4.7 (*s.e.* = 0.50) g live weight $m^{-2}$. Table 7 also shows that the mean live body weight varied between 0.1 and 0.3 mg with a summer minimum and an autumn/winter maximum.

### Respiration

The oxygen consumption rates per unit weight at +20°C and at daily mean soil temperatures are given in Table 8 together with the estimated daily mean oxygen consumption rates $m^{-2}$. Table 8 also presents the population respiration during the "summer" (244 days) and "winter" (122 days) period and during the whole annual period. The annual respiration was estimated at 42 (*s.e.* = 4.6) kcal $m^{-2}$.

Table 7. Abundance, biomass and live body weight of Enchytraeidae in 1971–72. Live weight is calculated as 5.56 times dry weight (Edwards, 1967).

| | no. $m^{-2}$ | | mg dry wt $m^{-2}$ | | mg live wt $ind^{-1}$ | |
|---|---|---|---|---|---|---|
| | $\bar{x}$ | s.e. | $\bar{x}$ | s.e. | $\bar{x}$ | s.e. |
| May 17 | 34 300 | 6 960 | 870 | 212 | 0.141 | 0.045 |
| June 15 | 27 400 | 5 280 | 556 | 109 | 0.113 | 0.031 |
| Sept 13 | 18 600 | 3 500 | 536 | 96 | 0.160 | 0.042 |
| Oct 28 | 21 500 | 3 180 | 1 075 | 153 | 0.278 | 0.057 |
| Nov 11 | 28 400 | 4 760 | 997 | 160 | 0.195 | 0.046 |
| "Summer" | 26 000 | 2 760 | 807 | 112 | | |
| "Winter" | 19 400 | 2 930 | 942 | 182 | 0.270 | 0.066 |
| Annual | 23 800 | 2 050 | 852 | 90 | | |

Table 8. Oxygen consumption rates of Enchytraeidae at different temperatures and the seasonal and annual respiration (kcal $m^{-2}$) in 1971–72.

| | Field temp. (°C) | $mm^3$ $O_2$ $g^{-1}$ $h^{-1}$ at field temp. | $cm^3$ $O_2$ $m^{-2}$ $day^{-1}$ | | kcal $m^{-2}$ | |
|---|---|---|---|---|---|---|
| | | | $\bar{x}$ | s.e. | $\bar{x}$ | s.e. |
| May 17 | +10.3 | 359 | 41.64 | 10.15 | | |
| June 15 | +10.3 | 387 | 28.69 | 5.63 | | |
| Sept 13 | + 7.7 | 311 | 22.23 | 3.99 | | |
| Oct 28 | + 5.0 | 239 | 34.26 | 4.88 | | |
| Nov 11 | + 1.4 | 172 | 22.83 | 3.65 | | |
| "Summer" | | | 29.93 | 3.66 | 35.05 | 4.28 |
| "Winter" | - 0.9 | 99 | 12.40 | 2.40 | 7.26 | 1.41 |
| Annual | | | 24.09 | 2.57 | 42.32 | 4.51 |

## Discussion

### Vertical distribution

Several studies on vertical distribution have revealed that a major part of the enchytraeids is usually found in the uppermost 6 cm of the soil profile (O'Connor, 1957; Peachey, 1963; Springett, 1963; Dash & Cragg, 1972b). Nielsen (1955b) found that about 70–99 % of the total enchytraeid number occurred in the upper 5 cm in most localities on sandy soils. However, in some habitats he reported a smaller percentage in the top 5 cm and a vertical distribution that was extended to deeper layers. Single individuals were observed as far as 70–75 cm below the surface. The vertical distribution at Spikbole resembles those in some of Nielsen's localities with a considerable number of enchytraeids occurring below the 12 cm level on some occasions. The enchytraeids may have occurred deeper than 20 cm during the "summer" period, but the underestima-

tion of the total population was probably small since the difficultly penetrated clay layer underlying the peat soil began at a depth of about 20 cm. This assumption was supported by the results from the "winter" period when although only 49 % of the enchytraeids were found in the top 12 cm of the soil profile, not more than 10 % occurred in the 20–28 cm level.

Nielsen (1955b), O'Connor (1957) and Springett *et al.* (1970) have shown that drought may affect the vertical distribution either by vertical migration or by different breeding and death rates at different depths. Nurminen (1967), who worked in Finnish coniferous forests, found that the vertical distribution of Enchytraeidae was concentrated in the litter and upper part of the humus during the spring, summer and autumn, when the soil temperature was above zero. During the winter the vertical distribution was concentrated in deeper layers. The change in the vertical distribution was observed at times when the temperature of the surface layer decreased below zero or rose above it (Nurminen, *op. cit.*). The seasonal variation in the vertical distribution at Spikbole was not very pronounced, but the mean depth seemed to be greater during the cold season than during the warm, which is thus in agreement with the findings of Nurminen (*op. cit.*). The early summer drought might have caused the low proportion of enchytraeids in the upper 0–4 cm in May and June.

### Abundance

The annual mean abundance of Enchytraeidae at Spikbole is similar to or lower than estimates from most other grassland soils. Ostbye *et al.* (1975) found mean abundances of 16 000 and 33 000 $m^{-2}$ in dry and wet alpine meadows in Norway, respectively, and Möller (1969) obtained annual means of about 20 000–45 000 $m^{-2}$ in three different grasslands in Germany. Annual mean abundances ranging from 30 000 to about 150 000 $m^{-2}$ have been recorded in Danish pastures (Nielsen, 1955b, 1961), in English high altitude grasslands (Peachey, 1963; Springett, 1970) and in an Alaskan meadow (Bunnell *et al.*, 1975). Both higher and lower abundances than those at Spikbole have been reported from coniferous forest soils in Finland (Huhta *et al.*, 1967; Nurminen, 1967), Norway (Abrahamsen, 1972) and Sweden (Axelsson *et al.*, 1973b).

The fluctuations in the enchytraeid numbers at Spikbole were not pronounced, but were partly in accordance with those reported by Nurminen (1967), who found summer and winter minima with spring and autumn maxima in-between. Distinct summer minima were found by Nielsen (1955c) in sandy soils in Denmark as a consequence of drought. Nurminen (*op. cit.*) recorded considerable variations in the year-to-year abundances. However, at Spikbole the abundance in October 1971 was similar to those in October 1969 (cf. Appendix 1). The abundance in May 1970 seemed to be lower than in May 1971, but the depths of the soil cores were probably insufficient in May 1970. Presupposing the same vertical distribution in May 1970 as in May 1971 the abundances would have been fairly equal, thus indicating small year-to-year changes.

### Biomass

The annual mean biomass was of the same order as the mean biomasses reported by Nielsen (1955b, 1961), Möller (1969) and Ostbye *et al.* (1975) for grassland soils, and by Abrahamsen (1973) for Norwegian coniferous forest soils. Higher biomasses in grasslands have been reported by Macfadyen (1963), Peachey (1963) and Bunnell *et al.* 1975).

## Respiration

Both Nielsen (1961) and O'Connor (1967, 1971) have presented laboratory data on oxygen consumption rates for enchytraeid species with representatives at Spikbole. Nielsen's primary data on these species were more extensive and more detailed in the smaller size classes, and it was therefore decided to base this study primarily on his figures. Nielsen (*op. cit.*) measured the oxygen uptake while the animals were moving about in a water film inside the respirometer. He concluded that the mechanical work of writhing and swimming inside the respirometer would only cause a small increment of respiration above the resting metabolism and that the respirometer data might be a slight underestimation of the field respiration, since enchytraeids have to force their way through the soil. More recently, Standen (1973) found that the oxygen consumption rate of actively moving *Cognettia sphagnetorum* was about twice that of passive animals, which is in accordance with the results on Collembola given by Zinkler (1966). She also observed that *C. sphagnetorum* became passive in response to low temperatures. Respirometer data based only on the active animals will thus give an overestimation of the field respiration according to Standen (1973) and a slight underestimation according to Nielsen (1961), assuming that the two authors have the same definition of "active" enchytraeids. In the present study Nielsen's data on oxygen consumption rates were used without any correction for different activity levels.

The oxygen consumption rate at +20°C was adjusted to ambient temperatures by using the correction curve presented by O'Connor (1971) for values between +5 and +20°C. The $Q_{10}$ values of the curve, about 1.4 between +5 and +10°C and 1.8 between +10 and +20°C, are relatively small in comparison with the $Q_{10}$ values of most other soil animals. However, they are in agreement with the results obtained by Williams *et al.* (1969), who found a $Q_{10} = 1.62$ between +10 and +20°C for the enchytraeid *Lumbricillus rivalis* (Lev.).

The non-linearity between oxygen consumption rate and live body weight when $b < 1$ in the equation $Q = a \cdot W^b$ may cause serious overestimations of oxygen consumption rates if an "average" individual is used for calculating the respiration of a whole population (cf. Berthet, 1971). The overestimation is insignificant if the body weights are fairly equal to the average weight, but the overestimation may be great in a sample with a wide range of size classes. The live body weights of the enchytraeids at Spikbole ranged from less than 10 μg to 5000 μg, and since the exponent $b$ was fairly low ($b = 0.67$) it is likely that the annual respiration of 42 (s.e. = 4.6) kcal $m^{-2}$ is an overestimation.

The annual respiration of Enchytraeidae at Spikbole falls within the range of respiration data, although most grassland estimates seem to be higher. Nielsen (1961) calculated the annual respiration to be 34, 48 and 155 kcal $m^{-2}$ in three grassland localities in Denmark, of which the latter was least affected by summer drought. Macfadyen (1963) reported annual respiration figures of 102 kcal $m^{-2}$ for a grazed meadow and 76 kcal $m^{-2}$ for a high-altitude grassland, both localities situated in England. Möller (1969) calculated annual respiration values of about 40 – 110 kcal $m^{-2}$ in three grasslands in Germany. Respiration figures from other ecosystems are very variable and, for example, Huhta & Koskenniemi (1975) calculated the annual respiration to be 2 – 10 kcal $m^{-2}$ in three spruce forest soils in Finland. Standen (1973) estimated the annual respiration of the dominant species *Cognettia sphagnetorum* to be 62 and 63 kcal $m^{-2}$ in two consecutive years in a high-altitude blanket bog in England, and O'Connor (1963, 1967) recorded an annual respiration of 149.5 kcal $m^{-2}$ in a coniferous forest soil in North Wales.

### Feeding habits

The feeding habits of Enchytraeidae have been reviewed by O'Connor (1967), who reported that enchytraeids may ingest different kinds of material, for example plant remains, Collembola droppings, algae, fungi and bacteria. However, he found it untenable that the soil-dwelling Enchytraeidae are primary decomposers of plant litter, since there is no evidence that they are able to digest complex structural polysaccharides (cf. Nielsen, 1962). Experiments made on *Cognettia sphagnetorum* suggest that this species "utilizes plant material that is already decomposing and has been preprocessed by microflora to remove toxins and to break down complex polysaccharides into simpler ones" (Whittaker, 1974). Some enchytraeid species may feed selectively on fungi (O'Connor, 1967; Dash & Cragg, 1972a), and it is possible that the soil enchytraeids mainly rely on microorganisms for food (cf. O'Connor, *op. cit.*). In the following synthesis the enchytraeids have been classified as saprovores/microbivores.

## LUMBRICIDAE

### Background

Lumbricidae is an oligochaete family which, in contrast to Enchytraeidae, is generally more abundant in neutral than in acid soils. Lumbricidae have been recorded in abundances of less than 1 $m^{-2}$ in moorlands and coniferous forests (Edwards & Lofty, 1972) up to more than 1000 $m^{-2}$ in a Saharan oasis (Dunger, 1964). The biomasses range from less than 1 to almost 500 g fw $m^{-2}$ (Dunger, *op. cit.*; Edwards & Lofty, *op. cit.*).

### Methods

The lumbricid soil cores were taken to a depth of 30 cm during the "summer" period and to 60 cm during the "winter" period. The cores were divided into an upper part (0–10 cm) and a lower part (10–30 cm) during the "summer" period. During the "winter" period the cores were divided into subcores from depths of 0–15, 15–30, 30–40, 40–50 and 50–60 cm. The sub-division was made in the field, after which the cores were transported to the laboratory, where they were sorted by hand. Several methods have been used for estimating the densities of lumbricid populations (Bouché, 1969; Satchell 1969) but ordinary hand sorting seems to be one of the most efficient methods, at least when deep-burrowing species such as *Lumbricus terrestris* L. are absent. The reliability of sorting lumbricid worms by hand was investigated by means of re-sorting soil samples from Spikbole (Axelsson *et al.*, 1971). The result showed that hand sorting gave satisfactory estimates of the number of large worms, while the number of worms weighing less than 0.2 g live body weight were probably underestimated. Totally about 80 % of the number and 96 % of the biomass were found in the first sorting, provided than the second sorting removed all remaining worms in the soil. The sorting efficiency was related to an average sorting time of 2.5 hours for sample units measuring 25 x 25 x 20 cm. The hand sorting time for the 25 x 25 x 30 cm units in the present study was about 3 hours, which indicated that about

the same sorting efficiency could be expected as in the earlier study. The sorting time was prolonged during the "winter" (10.5 hours per soil core) owing to greater core depths and more difficulty sorted soil in the deeper layers.

After the hand sorting the earthworms were cleaned of soil in water and killed by being placed in 6 % formalin for five minutes. The worms were rinsed in water before the identification and were then dried at +60°C in a vacuum drier. The individual dry weights, including the gut content, were determined to the nearest 0.01 mg. Sometimes a part of a worm was cut off during the sampling. Anterior parts with at least 15 segments and complete posterior parts beginning in front of segment 15 were counted as worms. Heads, tails and mid-parts were, thus, omitted from the estimation of abundance, but they were included in the biomass estimates.

The primary data on the earthworm biomass had to be corrected for mucus secretion. *Allolobophora rosea* (Sav.) secreted large quantities of mucus when placed in formalin. The amount of mucus loss was studied on 54 different sized (0.02–1.13 g live body weight) *A. rosea* specimens taken from the research plot and placed in 6 % formalin for five minutes. The formalin was filtered off from the mucus, which was dried in the same way as the earthworms. The mucus loss amounted to 13.1 % of the dried worms and, thus, 11.6 % of the initial dry weight. The mucus losses of the other lumbricid species at Spikbole were neglected, since no visible secretion was observed in the formalin.

Corrections were also made for gut content. During the summer 25 active *A. rosea* specimens representing all size-classes were taken from the research plot, killed in 6 % formalin and dissected. The dry weight gut content ranged from 1.2 to 30.1 % with a mean of 13.15 (*s.e.* = 1.37) % of the dry weight obtained, which corresponds to a gut content of 11.8 % of the initial dry weight when the mucus loss was considered. This value was almost equal to that of the mucus loss of 11.6 %. Consequently, the gut content weight was nearly balanced by the mucus loss, and since the fact that the gut content weight may vary over the year was disregarded, no correction of the dry weights obtained was made for *A. rosea*. Similar determinations of the other earthworm species showed that the gut content of *A. caliginosa* (Sav.) was 15 % of the total dry weight, and the corresponding value for *Dendrobaena* and *Lumbricus* species was 10 %. Corrections owing to the gut content were made for these species.

The oxygen consumption rates of *A. rosea* were calculated from the determinations reported by Phillipson & Bolton (1976). They divided the *A. rosea* population into three size classes, "small immatures" (< 0.1 g fw), "large immatures" (> 0.1 g fw without clitellum) and adults (with fully developed clitellum), in each of which the respiratory rate per unit weight was not suggested to be affected by differences in body weight. Phillipson & Bolton (*op. cit.*) found that the carbon dioxide evolution rates, respiratory quotients and oxygen consumption rates varied with size class and season although determined at the same temperature. In the present study, however, these seasonal variations were neglected, and the annual mean oxygen consumption rates were used. These rates were 78.56, 72.66 and 64.17 $mm^3$ $O_2$ $g^{-1}$ live weight $h^{-1}$ at +10°C for small immatures, large immatures and adults, respectively. Since the gut content on average accounted for 25 % of the total live weight (Phillipson & Bolton, *op. cit.*), the equivalent mean oxygen consumption rates for worms with empty guts were 104.75, 96.88 and 85.56 $mm^3$ $O_2$ $g^{-1}$ live weight $h^{-1}$ at +10°C for the size classes, respectively. According

to Phillipson & Bolton (*op. cit.*) the $Q_{10}$ values between +6 and +15°C were 1.96, 2.42 and 1.42 for the three size classes, respectively, and the pooled values for all size classes implied a $Q_{10}$ of 2.05 between these temperatures. In the present investigation the oxygen consumption rates at +10°C for worms with empty guts were corrected to actual field temperatures by using a $Q_{10} = 2$ down to +5°C. The oxygen consumption rates at temperatures below +5°C were calculated according to a $Q_{10} = 3$. The oxygen consumption rates of quiescent (dormant) *A. rosea* were probably lower than those of active worms (cf. Gallissian, 1967), and were assumed to be half of those of active worms.

The oxygen consumption rates of the other lumbricid species at Spikbole were calculated according to Byzova (1965). Byzova (*op. cit.*) estimated the relationship between oxygen uptake rate and live body weight of adult earthworms at +19°C to be $Q = 78 \cdot W^{0.91}$ for *A. caliginosa*, $Q = 119 \cdot W^{0.71}$ for *Dendrobaena octaedra* (Sav.) and $Q = 93 \cdot W^{0.84}$ for *Lumbricus rubellus* Hoffm., where $Q$ was $mm^3$ $O_2$ $ind^{-1}$ $h^{-1}$ and $W$ was g live body weight. In the present study these equations were used for adults as well as immatures, and the equation for *D. octaedra* was also used for *D. rubida* (Sav.). The oxygen consumption rate was calculated for each of the individuals in the samples, and therefore no size-class division was needed. Temperature corrections were made assuming an exponential relationship between temperature and oxygen consumption rate with $Q_{10} = 2$ for temperatures down to +5°C and $Q_{10} = 3$ for temperatures below +5°C. The winter temperatures was considered to be −0.9°C (measured at a depth of 5 cm) for the *Dendrobaena* species, but since the other earthworm species descended below the frost a winter temperature of 0°C was used for *A. rosea*, *A. caliginosa* and *L. rubellus*.

The oxygen consumption rates had to be calculated from the gut-content-free live body weights, and therefore the live weight/dry weight ratio had to be estimated. The live weight/dry weight ratio for *A. rosea* was studied in August 1972, October 1972 and 1973, and June 1974. The mean ratios varied between 5 and 6 for worms with empty gut. The mean value of 61 specimens was 5.5, and this ratio was used for obtaining live body weights of all lumbricid species.

Byzova (1966) has demonstrated that surface-active species such as *D. octaedra* are susceptible to a drop in oxygen tension, while soil-dwelling species as *A. caliginosa* and *A. rosea* do not reduce their respiratory rate even at very low oxygen concentrations. Since the *Dendrobaena* species were never found at greater depths at Spikbole there was no need to correct the respiratory rates for changes in the oxygen content of the soil atmosphere.

## Results

### Species composition

Five lumbricid species were found at Spikbole, namely *Allolobophora caliginosa*, *A. rosea*, *Dendrobaena octaedra*, *D. rubida* and *Lumbricus rubellus*. Adult *D. rubida* belonged to *D. rubida* f. *subrubicunda* (Eisen), while juvenile *D. rubida* were not identified to the subspecies level. The nomenclature follows Gerard (1964).

## Vertical distribution

The *Dendrobaena* species were always found in the litter and the upper 10–15 cm of the soil (Fig. 13) and did not seem to migrate downwards due to drought or cold. The deep-burrowing species *A. rosea* and *A. caliginosa* were concentrated in the upper 10 cm of the soil profile in May, but were generally found deeper on the other sampling occasions. Obviously they migrated to deeper layers when the top soil conditions became unfavourable. During the "winter" all *A. rosea* specimens were found below the frozen soil which reached a depth of 15 -18 cm. Occasionally individuals of *A. rosea* were observed at a depth of 55 cm during the late winter, which was just above the ground water table of 60 cm at that time. The vertical distribution of *A. rosea* and *A. caliginosa* was extended to deeper layers also in June, when a majority of the specimens were found at a depth of 15–20 cm. The vertical distribution of *L. rubellus* was intermediate to those of the *Dendrobaena* and *Allolobophora* species.

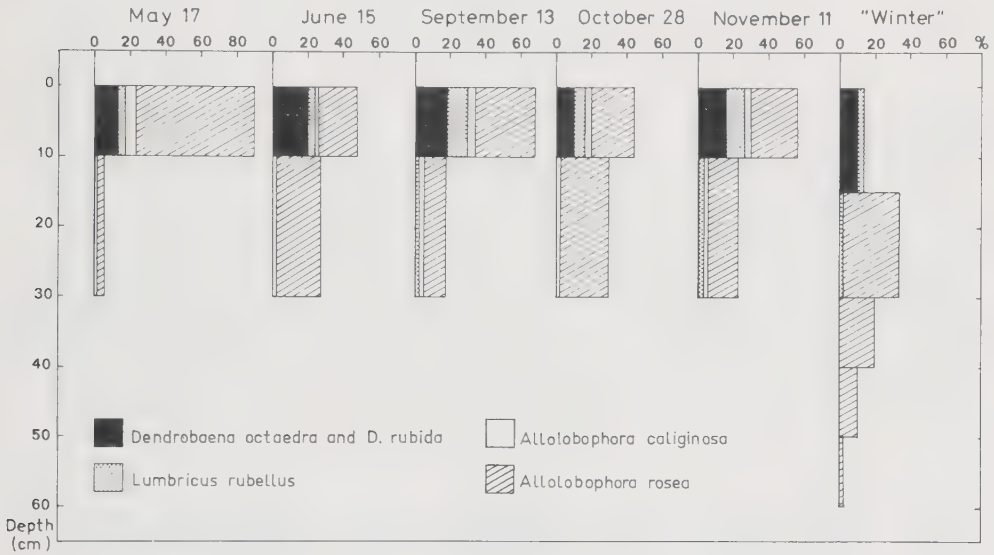


**Figure 13.** The vertical distribution of Lumbricidae in 1971–72. The numbers of lumbricids per 10 cm vertical layers are expressed as percentages of the total number on each sampling occasion.

## Abundance

The most abundant species at Spikbole was *A. rosea* with an annual mean density of 95 (*s.e.* = 11) specimens $m^{-2}$ (Table 9). The abundances fluctuated between 65 and 122 $m^{-2}$ at the different samplings, but the apparent differences were probably caused by random effects (high standard errors) or varying efficiency in sorting juvenile worms. The number of adult *A. rosea* was, notwithstanding, fairly constant with about 30–40 specimens $m^{-2}$ on most sampling occasions (Table 11). *D. octaedra* was also relatively abundant with 21 (*s.e.* = 3.5) specimens $m^{-2}$, while the other species were more sparse (Table 9). The annual mean abundance of all lumbricid species was 133 (*s.e.* = 11) $m^{-2}$.

Table 9. Abundance (no. $m^{-2}$) of Lumbricidae in 1971–72. Standard error is given within parentheses below the corresponding mean value.

| | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|
| *Allolobophora caliginosa* | 10.7 | 4.3 | 9.6 | 8.5 | 6.9 | 8.0 | 1.1 | 5.7 |
| | (4.6) | (2.5) | (4.4) | (3.8) | (4.7) | (1.2) | (0.8) | (0.8) |
| *A. rosea* | 92.8 | 75.7 | 68.3 | 102.4 | 65.1 | 80.9 | 121.7 | 94.5 |
| | (36.0) | (21.6) | (21.6) | (33.5) | (27.9) | (7.3) | (27.6) | (10.4) |
| *Dendrobaena octaedra* | 12.8 | 19.2 | 18.1 | 8.5 | 12.6 | 14.2 | 33.4 | 20.6 |
| | (5.5) | (11.9) | (8.0) | (3.8) | (3.0) | (2.0) | (9.6) | (3.5) |
| *D. rubida* | 2.1 | 1.1 | 5.3 | 3.2 | 3.4 | 3.0 | 2.6 | 2.9 |
| | (2.1) | (1.1) | (4.4) | (2.3) | (2.5) | (0.8) | (2.6) | (1.0) |
| *Lumbricus rubellus* | 6.4 | 5.3 | 12.8 | 9.6 | 14.8 | 9.8 | 8.5 | 9.4 |
| | (4.4) | (2.6) | (3.9) | (5.8) | (3.5) | (1.9) | (3.2) | (1.7) |
| Lumbricidae, total | 124.8 | 105.6 | 114.1 | 132.3 | 102.8 | 115.9 | 167.2 | 133.0 |
| | (36.2) | (23.4) | (26.4) | (31.9) | (30.1) | (5.6) | (28.6) | (10.3) |

## Biomass

The annual mean biomass of Lumbricidae was dominated by *A. rosea* with 5.0 (*s.e.* = 0.5) g dw $m^{-2}$, which accounted for 84 % of the total lumbricid biomass of 5.9 (*s.e.* = 0.5) g dw $m^{-2}$ (Table 10). The biomass fluctuations for *A. rosea* were fairly small which could partly be assigned to the relatively constant proportion of adults. The adults of *A. rosea* contributed 79 % to the total biomass of this species (Table 11). The mean body weight of adult *A. rosea* was about 600 mg live weight during the whole study period. *L. rubellus*, *A. caliginosa*, *D. octaedra* and *D. rubida* accounted for 6, 5, 4 and 0.7 % of the total lumbricid biomass, respectively.

Table 10. Biomass (g dry weight $m^{-2}$) of Lumbricidae in 1971–72. Corrections are included for mucus loss and gut content. Standard error is given within parentheses below the corresponding mean value.

| | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|
| *Allolobophora caliginosa* | 0.64 | 0.23 | 0.63 | 0.32 | 0.29 | 0.42 | 0.06 | 0.30 |
| | (0.25) | (0.14) | (0.28) | (0.19) | (0.20) | (0.09) | (0.05) | (0.07) |
| *A. rosea* | 4.85 | 5.23 | 4.49 | 6.43 | 4.62 | 5.12 | 4.70 | 4.98 |
| | (1.13) | (1.47) | (1.47) | (1.97) | (2.11) | (0.35) | (1.28) | (0.49) |
| *Dendrobaena octaedra* | 0.23 | 0.32 | 0.28 | 0.12 | 0.15 | 0.22 | 0.27 | 0.24 |
| | (0.09) | (0.21) | (0.12) | (0.06) | (0.06) | (0.04) | (0.07) | (0.04) |
| *D. rubida* | 0.04 | 0.01 | 0.15 | 0.06 | 0.03 | 0.06 | 0.01 | 0.04 |
| | (0.04) | (0.01) | (0.10) | (0.06) | (0.03) | (0.03) | (0.01) | (0.02) |
| *Lumbricus rubellus* | 0.62 | 0.29 | 0.51 | 0.18 | 0.64 | 0.45 | 0.21 | 0.37 |
| | (0.05) | (0.16) | (0.32) | (0.10) | (0.21) | (0.10) | (0.09) | (0.07) |
| Lumbricidae, total | 6.39 | 6.07 | 6.06 | 7.11 | 5.74 | 6.27 | 5.25 | 5.93 |
| | (1.19) | (1.36) | (1.59) | (1.93) | (2.19) | (0.24) | (1.29) | (0.46) |

Table 11. Abundances, biomasses and oxygen consumption rates of different size classes of *Allolobophora rosea*. Small immatures < 0.1 g live body weight, large immatures ⩾ 0.1 g live body weight without fully formed clitella, and adults with fully formed clitella. The rates in June and the "winter" are reduced to 75 % due to quiescence (see text).

| | no. $m^{-2}$ | | g live wt $m^{-2}$ | | $mm^3$ $O_2$ $g^{-1}$ $h^{-1}$ | $cm^3$ $O_2$ $m^{-2}$ $day^{-1}$ | |
|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | s.e. | $\bar{x}$ | s.e. | at field temp. | $\bar{x}$ | s.e. |
| **May 17** | | | | | | | |
| Small immatures | 34.2 | 17.2 | 1.38 | 0.66 | 107.0 | 3.54 | 1.70 |
| Large immatures | 23.5 | 11.5 | 4.75 | 1.96 | 98.9 | 11.27 | 4.65 |
| Adults | 35.2 | 9.4 | 20.53 | 4.78 | 87.4 | 43.05 | 10.01 |
| **June 15** | | | | | | | |
| Small immatures | 28.8 | 10.9 | 1.23 | 0.42 | 80.2 | 2.37 | 0.80 |
| Large immatures | 11.7 | 5.1 | 4.46 | 1.66 | 74.2 | 7.94 | 2.96 |
| Adults | 35.2 | 10.8 | 23.06 | 6.42 | 65.5 | 36.25 | 10.10 |
| **September 13** | | | | | | | |
| Small immatures | 11.7 | 3.7 | 0.53 | 0.16 | 89.3 | 1.14 | 0.34 |
| Large immatures | 20.3 | 9.3 | 4.19 | 1.83 | 82.6 | 8.31 | 3.63 |
| Adults | 36.3 | 11.9 | 19.95 | 6.58 | 73.0 | 34.93 | 11.51 |
| **October 28** | | | | | | | |
| Small immatures | 30.9 | 16.4 | 1.45 | 0.86 | 74.1 | 2.58 | 1.53 |
| Large immatures | 21.3 | 7.4 | 4.14 | 1.42 | 68.5 | 6.80 | 2.33 |
| Adults | 50.1 | 15.0 | 29.78 | 9.28 | 60.5 | 43.24 | 13.48 |
| **November 11** | | | | | | | |
| Small immatures | 13.7 | 7.3 | 0.62 | 0.36 | 49.9 | 0.75 | 0.43 |
| Large immatures | 19.4 | 9.7 | 4.61 | 2.45 | 46.1 | 5.10 | 2.71 |
| Adults | 32.0 | 15.0 | 20.16 | 9.90 | 40.7 | 19.71 | 9.68 |
| **"Summer" means** | | | | | | | |
| Small immatures | 23.9 | 4.7 | 1.04 | 0.20 | | 2.07 | 0.51 |
| Large immatures | 19.2 | 2.0 | 4.43 | 0.12 | | 7.89 | 1.02 |
| Adults | 37.8 | 3.2 | 22.70 | 1.86 | | 35.44 | 4.29 |
| **"Winter"** | | | | | | | |
| Small immatures | 60.3 | 16.3 | 2.28 | 0.57 | 32.1 | 1.75 | 0.44 |
| Large immatures | 26.0 | 5.6 | 4.27 | 1.03 | 29.7 | 3.04 | 0.74 |
| Adults | 35.3 | 10.7 | 19.29 | 6.31 | 26.2 | 12.13 | 3.97 |
| **Annual means** | | | | | | | |
| Small immatures | 36.0 | 6.3 | 1.45 | 0.23 | | 1.97 | 0.37 |
| Large immatures | 21.5 | 2.3 | 4.38 | 0.36 | | 6.27 | 0.72 |
| Adults | 36.9 | 4.2 | 21.56 | 2.44 | | 27.67 | 3.15 |

## Respiration

About half the number of the *A. rosea* specimens were quiescent on June 15 and during the "winter", and therefore the oxygen consumption rates on these occasions were assumed to be markedly reduced. The reduction was made similarly for all size classes. The oxygen consumption rates for different size classes of *A. rosea* and different sampling occasions are presented in Table 11. The adults accounted for 77 % of the annual respiration of *A. rosea*, although both the small and large juveniles had somewhat higher oxygen consumption rates per unit weight than the adults. The annual respiration of *A. rosea* amounted to 63 (*s.e.* = 7.0) kcal $m^{-2}$ (Table 12). No quiescence was observed in *D. octaedra, L. rubellus, A. caliginosa* or *D. rubida*, although *A. caliginosa* are often reported to be quiescent during unfavourable conditions. These species had a total annual respiration of about 12 kcal $m^{-2}$, and as a whole the lumbricids at Spikbole respired 75 (*s.e.* = 8.2) kcal $m^{-2}$ $yr^{-1}$.

Table 12. Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) and the annual respiration (kcal $m^{-2}$) of Lumbricidae in 1971–72. Standard error is given within parentheses below the corresponding mean value.

| | Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) | | | | | | | | Annual respiration (kcal $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|
| | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual | |
| *Allolobophora caliginosa* | 3.97 | 1.42 | 3.20 | 1.37 | 0.84 | 2.16 | 0.15 | 1.49 | 2.62 |
| | (1.37) | (0.87) | (1.41) | (0.75) | (0.55) | (0.61) | (0.12) | (0.41) | (0.71) |
| *A. rosea* | 57.86 | 46.56 | 44.39 | 52.63 | 25.56 | 45.40 | 16.92 | 35.91 | 63.08 |
| | | | | | | (5.50) | (4.52) | (3.96) | (6.96) |
| *Dendrobaena octaedra* | 3.78 | 5.45 | 4.01 | 1.48 | 1.28 | 3.20 | 1.93 | 2.78 | 4.88 |
| | (1.48) | (3.52) | (1.67) | (0.65) | (0.43) | (0.80) | (0.49) | (0.56) | (0.98) |
| *D. rubida* | 0.69 | 0.20 | 1.89 | 0.64 | 0.31 | 0.75 | 0.09 | 0.53 | 0.92 |
| | (0.69) | (0.20) | (1.30) | (0.59) | (0.24) | (0.31) | (0.09) | (0.21) | (0.36) |
| *Lumbricus rubellus* | 4.70 | 2.20 | 3.31 | 1.16 | 2.44 | 2.76 | 0.74 | 2.09 | 3.67 |
| | (3.23) | (1.14) | (1.84) | (0.60) | (0.77) | (0.60) | (0.29) | (0.41) | (0.72) |
| Lumbricidae, total | 71.00 | 55.84 | 56.81 | 57.28 | 30.44 | 54.27 | 19.83 | 42.79 | 75.18 |
| | | | | | | (6.58) | (4.54) | (4.64) | (8.15) |

## Cocoons

No particular attention was paid to the abundance, biomass and respiration of lumbricid cocoons in this study. During the "winter" the abundance based on hand sorting was estimated at 150 (*s.e.* = 42) cocoons $m^{-2}$, of which the *A. rosea* cocoons amounted to 100 (*s.e.* = 34) $m^{-2}$. The mean weight of *A. rosea* cocoons was about 14 mg fw or 3 mg dw, which corresponds to a biomass of 0.3 (*s.e.* = 0.1) g dw $m^{-2}$. Most of the other cocoons belonged to *D. octaedra* with a mean fresh weight of 3.5 g. Phillipson & Bolton (1976) estimated the oxygen consumption rates of *A. rosea* cocoons at +5°C, +10°C and +15°C to be 21.47, 27.44 and 32.02 $mm^3$ $O_2$ $g^{-1}$ fw $h^{-1}$, respectively. The magnitude of *A. rosea* cocoon respiration was estimated to be 1.26 kcal $m^{-2}$ $yr^{-1}$, assuming the same number (100) $m^{-2}$ on all sampling occasions and the same temperature relationship ($Q_{10}$ = 1.63) as given by Phillipson & Bolton (*op. cit.*) also

for temperatures below +5°C. The annual respiration of the other cocoons was about 0.16 kcal $m^{-2}$, provided that all these cocoons belonged to *D. octaedra*, and assuming that the respiratory rate per unit weight was the same as that of *A. rosea*. On these assumptions, the total cocoon respiration could be placed at the very approximate figure of 1.4 kcal $m^{-2}$ $yr^{-1}$, which was almost 2 % of the total lumbricid respiration.

## Discussion

### Vertical distribution

The vertical distribution of lumbricids has been studied by Gerard (1967), Nordström & Rundgren (1973) and Rundgren (1975), among others. A general pattern is that vertical migrating earthworms such as *A. rosea* and *A. caliginosa* seem to avoid very cold and very dry surface soil, which is in agreement with the findings at Spikbole. Cold apparently had the greatest influence on the vertical distribution of these species at Spikbole, although reservations must be made for the influence of drought during the part of the summer when no sampling was performed. However, Rundgren (*op. cit.*) found that the vertical migration of *Allolobophora* spp. in a permanent pasture in southern Sweden was much more pronounced due to the winter cold than due to the summer drought.

### Abundance

Few, if any, worms could have hatched after the October and November samplings because of the low soil temperatures (cf. Edwards & Lofty, 1972), and the high mean number of juvenile *A. rosea* (cf. Table 11) during the "winter" was probably an effect of more efficient hand sorting due to the prolonged sorting time. This could also be true for the small species *D. octaedra*, which was also obtained in higher numbers during the "winter" than at any of the "summer" samplings. However, the number of adult *A. rosea* during the "winter" was similar to that obtained during the "summer" period, which supports the assumption that the hand sorting efficiency was probably high on all sampling occasions for large worms (cf. Axelsson *et al.*, 1971). Owing to the insufficient sorting efficiency of small worms the annual mean abundance of about 130 lumbricids $m^{-2}$ must be considered as a slight underestimation.

The lumbricid abundances obtained at Spikbole are similar to the abundances in many other temperate grasslands. Thus, Nordström & Rundgren (1973) found densities of 29–148 $m^{-2}$ in different localities in southern Sweden, Bengtson *et al.* (1975) recorded abundances from 3 $m^{-2}$ in grass heaths to 312 $m^{-2}$ in grass meadows in Iceland. Baltzer (1956) obtained a range of 6–282 $m^{-2}$ in pasture and meadow land in Germany, Ghilarov & Chernov (1974) reported densities of 12–216 $m^{-2}$ in various steppe habitats in the USSR, and Nowak (1975) estimated the abundance to be 83–99 $m^{-2}$ in a grazed pasture in Poland. Somewhat higher grassland abundances were found by Reynoldson (1955) in North Wales (441–484 $m^{-2}$), Svendsen (1957) in upland localities in England (384–470 $m^{-2}$), Barley (1959) in Australia (260–740 $m^{-2}$), Zajonc (1970) in Slovakia (203 $m^{-2}$), Atlavinytė (1973) in Lithuania (185 $m^{-2}$), Nowak (1975) in a former sheep-fold in Poland (223–591 $m^{-2}$) and Curry (1976) in Ireland (203

310 $m^{-2}$), among others. These data indicate that the average lumbricid density for temperate grassland is in the region of 200 $m^{-2}$. The abundance obtained at Spikbole is thus in the lower part of the grassland range.

### Biomass

The underestimation of the biomass at Spikbole was probably small since the biomass was dominated by adult *A. rosea*, which were efficiently hand sorted. The annual mean biomass of about 6 g dw $m^{-2}$ or about 30–35 g fw $m^{-2}$ of total Lumbricidae at Spikbole falls within the range of biomass given by Baltzer (1956), Atlavinytė (1973), Nordström & Rundgren (1973), Bengtson *et al.* (1975) and Nowak (1975) for other grassland soils. Higher biomasses in grasslands have been found by, for example, Reynoldson (1955), Svendsen (1957), Barley (1959) and Curry (1976).

### Respiration

Published data on respiratory rates of earthworms have mostly been concerned with adult worms, while data on immature worms are often lacking. One exception is Phillipson & Bolton's (1976) data on immature *A. rosea*, while the respiration rates on most other juveniles have to be extrapolated from determinations on adults. Very few respiration determinations have been published on quiescent and diapausing earthworms. However, Gallissian (1967) found that the oxygen consumption rate of the lumbricid *Eophila dollfusi* Tétry at diapause was reduced to about half that of active worms. The same relationship between the rates at quiescence and activity was used for *A. rosea*, although this species has not a true diapause (Satchell, 1967).

The estimates of lumbricid respiration in grasslands are very few in comparison with the numerous data on lumbricid abundance and biomass. The annual respiration of around 75 kcal $m^{-2}$ $yr^{-1}$ for total Lumbricidae at Spikbole is higher than the respiration figure (22 kcal $m^{-2}$ $yr^{-1}$) given by Nowak (1975) for a grazed pasture in Poland. On the other hand, it is lower than the estimate (103 kcal $m^{-2}$ $yr^{-1}$) for a former sheep-fold pasture in Poland (Nowak, *op. cit.*). Higher respiration figures were also reported by Macfadyen (1963) for a grazed meadow in England (178 kcal $m^{-2}$ $yr^{-1}$) and an upland grassland also in England (333 kcal $m^{-2}$ $yr^{-1}$). These respiration figures to a great extent reflect the differences in biomass, but different ways of calculating the respiration rates also have a considerable influence on the final estimates (cf. General discussion, p. 147).

### Feeding habits

Earthworms both ingest soil and decaying plant litter. Many species also show ability to distinguish between different kinds of litter due to its palatability (Satchell, 1967; Satchell & Lowe, 1967). The consumption of plant litter does not necessarily imply that the earthworms assimilate the dead plant material, since they may also feed on the microorganisms attached to the litter. However, enzymatic studies have shown that litter feeding species such as *Dendrobaena octaedra* and *Lumbricus terrestris* are able to degrade cellulose (Nielsen, 1962; Satchell, 1967), thus indicating true saprovory for these species, while the soil-inhabiting species *Allolobophora rosea* seems to be unable to digest cellulose (Nielsen, *op. cit.*). Some earthworms such as *Allolobophora caliginosa* were found to digest soil algae (Atlavinytė & Pociené, 1973), although Waters (1955) suggested that this species chiefly feeds on dead roots. However, the Lumbricidae species at Spikbole were all classified as saprovores/microbivores.

# DIPLOPODA

## Background

Diplopods are considered to be important soil animals in many temperate habitats. Dunger (1964) reported peak populations of 200–300 individuals $m^{-2}$ in moist woodland leaf litter and more than 500 $m^{-2}$ in well fertilized agricultural soils, but the densities are often much lower. The biomass of Diplopoda can be very high in certain localities and, according to Bornebusch (1930), a population of 177 diplopods $m^{-2}$ corresponded to a biomass of 7.5 g fw $m^{-2}$ in a Danish beech mull soil.

## Methods

The diplopods at Spikbole were separated from the lumbricid soil cores by means of hand sorting, after which they were identified, counted and dried at +60°C in a vacuum-drier. The dry weights were determined to the nearest 0.01 mg. The gut content weight was neglected.

The oxygen consumption rates were calculated for each individual according to the equation $Q = 36.5 \cdot W^{0.73}$, where $Q$ denotes $mm^3$ $O_2$ $ind^{-1}$ $h^{-1}$ and $W$ denotes g live body weight. This equation was originally given by Byzova (1973) for the iulid *Sarmatiulus kessleri* Lohm. at +20°C. Temperature corrections were made assuming an exponential relationship between temperature and oxygen consumption rate with a $Q_{10} = 2$ for temperatures between +20°C and +5°C. Below +5°C the respiratory rates, owing to the lack of measurement data, were assumed to decrease linearly with the temperature to a zero-value at −5°C (cf. Enchytraeidae, p. 40). The live body weights of Diplopoda were calculated using a dry weight/live weight ratio of 0.455 according to Edwards (1967).

## Results

The only diplopod species found at Spikbole was the iulid *Schizophyllum sabulosum* L. It was mainly sorted from the uppermost litter and soil layers. The estimates of abundance, biomass and population respiration are given in Table 13. The estimates are fairly imprecise, since they are based on very few specimens. The annual mean number was estimated at 1.8 (*s.e.* = 0.8) $m^{-2}$, the annual mean biomass was 29 (*s.e.*= 16) mg dw $m^{-2}$ and the annual respiration was calculated to be 0.06 (*s.e.* = 0.03) kcal $m^{-2}$.

## Discussion

The low number of diplopods in the samples made it impossible to detect any real population fluctuations. The hand-sorting method was probably not sufficiently accurate for estimating the number of small diplopods, although some newly hatched *Schizophyllum sabulosum* juveniles were found in September. The other specimens obtained were bigger and probably much older since *S. sabulosum* attains maturity some 3 years after hatching and then may survive for another 1–3 years (Halkka, 1958).

The oxygen consumption rate of *S. sabulosum* has been measured by Byzova (1967), but this determination was not used here since it was based on relatively few individuals

Table 13. Abundance, biomass, oxygen consumption rates and the seasonal and annual respiration of Diplopoda in 1971–72.

| | no. $m^{-2}$ | | mg dry wt $m^{-2}$ | | $cm^3$ $O_2$ $m^{-2}$ $day^{-1}$ | | kcal $m^{-2}$ | |
|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | s.e. | $\bar{x}$ | s.e. | $\bar{x}$ | s.e. | $\bar{x}$ | s.e. |
| May 17 | 1.1 | 1.1 | 34.3 | 34.3 | 0.069 | 0.069 | | |
| June 15 | 1,1 | 1,1 | 34.1 | 34.1 | 0.069 | 0.069 | | |
| Sept 13 | 5.3 | 5.3 | 0.5 | 0.5 | 0.004 | 0.004 | | |
| Oct 28 | 0 | | 0 | | 0 | | | |
| Nov 11 | 1.1 | 1.1 | 14.4 | 14.4 | 0.016 | 0.016 | | |
| "Summer" | 1.7 | 1.0 | 16.7 | 7.7 | 0.032 | 0.016 | 0.037 | 0.018 |
| "Winter" | 1.8 | 1.4 | 53.8 | 42.7 | 0.031 | 0.025 | 0.018 | 0.015 |
| Annual | 1.8 | 0.8 | 29.0 | 15.1 | 0.031 | 0.014 | 0.055 | 0.024 |

of equal size. It was preferred to calculate the oxygen consumption rates of *S. sabulosum* from those of the related species *Sarmatiulus (= Schizophyllum) kessleri* given by Byzova (1973), since the values of the last mentioned species were based on more extensive observations. Byzova (1967) recorded a $Q_{10}$ = 2 for *S. sabulosum* between +7 and +17°C, and here the same $Q_{10}$ value was used for correcting the oxygen consumption rate to the actual field temperature down to +5°C by assuming an exponential relationship. However, Byzova (1971) reported considerable deviations from the exponential curve for *S. kessleri* and *Amblyiulus continentalis* Attems., and it is possible that such deviations also exist for *S. sabulosum*.

The annual respiration of Diplopoda at Spikbole was very low (0.06 kcal $m^{-2}$ $yr^{-1}$) due to the low population level. Much higher values have been reported from a grazed meadow in England, where Macfadyen (1963) calculated the annual respiration to be 95.4 kcal $m^{-2}$ $yr^{-1}$ for a biomass of 12.5 g fw $m^{-2}$. This figure is, however, based on a respiration rate per unit weight that is about eight times higher than that at Spikbole. High respiration figures have also been obtained by Saito (1970), who calculated the annual respiration of the diplopod *Japonaria laminata armigera* to be 1.51 and 30.9 kcal $m^{-2}$ $yr^{-1}$ during two different years in an evergreen broad-leaf forest in central Japan.

*S. sabulosum* is a surface-living species, which is often observed feeding on the aerial parts of the vegetation (Blower, 1955), but it is also considered as a litter feeder (Byzova, 1967). *S. sabulosum* may thus be classified as a herbivore or a saprovore or both, but in the following synthesis it has only been considered as a saprovore/microbivore.

## COLLEMBOLA

### Background

Collembola is an arthropod group that is distributed throughout the world and often occurs in great densities. Most of its members belong to the soil fauna, although some

species occur in a variety of other habitats. The abundances in the litter and soil range from 10 000 to 100 000 $m^{-2}$ in many localities (Hale, 1967; Curry, 1969; Tanaka, 1970a; Healey, 1971), but much lower densities have been recorded in the tropics (e.g. Block, 1970). Peak values of 200 000–300 000 collembolans $m^{-2}$ have been reported by Naglitsch (1963) in Germany, Tilbrook (1967) in Maritime Antarctic, McMillan (1969) in New Zealand, Tanaka (1970b) in Japan, Bengtson *et al.* (1974) in Spitsbergen and Vtorov & Martynova (1974) in Tien-Shan. Extremely high densities have been reported by Collins *et al.* (1975) in algal subformations on Signy Island in Maritime Antarctic, where the annual mean was estimated at 670 000 $m^{-2}$ and the summer mean was estimated at 959 000 $m^{-2}$. Biomass estimates are considerably scarcer in the literature than abundance estimates, which is probably owing to the difficulty of obtaining reliable weight determinations of small Collembola. Many authors have recorded biomasses of about 200–500 mg fw $m^{-2}$ (cf. references in Tanaka, 1970a; Petersen, 1972), which correspond to about 70–170 mg dw $m^{-2}$.

## Methods

The estimates of most of the Collembola species were based on samplings with the microarthropod sampler followed by high gradient canister extraction. Sparsely occurring species were assumed to be estimated with a fairly low precision when based on the small microarthropod corer. Hence, the larger macroarthropod sampler in combination with Tullgren funnel extraction was used as an alternative from June onwards in order to estimate the abundance of mobile and surface-living species with a higher precision. During the winter the snow lying on top of the soil and litter cores was also taken with the macroarthropod sampler. The snow was melted separately in the laboratory and searched for collembolans. After the extractions the collembolans were identified, counted and measured to the nearest 0.02 mm using a stereo-microscope fitted with a micrometer eyepiece to obtain the individual body lengths. The body lengths were used to calculate the body dry weights according to the regression equations given by Tanaka (1970a) and Petersen (1975). The equations were of the form $\log W = \log a + b \log L$, where $W$ denotes the dry body weight in $\mu$g of an individual of $L$ mm length, and where $a$ and $b$ are constants. The constants used for the Collembola species at Spikbole are given in Table 14. Species found at Spikbole but not investigated by Tanaka or Petersen were given the same equation as species with similar body shape. The body length was measured on all individual collembolans in the samples.

The oxygen consumption rates of the collembolans at Spikbole were calculated from laboratory measurements made by a number of investigators (Table 15). The determinations were adjusted to +18°C by assuming an exponential relationship between temperature and oxygen uptake. The 29 values given in Table 15 were used to calculate the relationship between log live body weight and log oxygen consumption rate at +18°C according to the method of least squares. The individual values and the regression line best fitted to the values are illustrated in Fig. 14. The equation obtained was $Q = 63 \cdot W^{0.73}$, in which $Q$ was $mm^3$ $O_2$ $ind^{-1}$ $h^{-1}$ and $W$ was g live body weight. This equation was used for calculating the oxygen consumption rates of all Collembola species at Spikbole. Temperature corrections were made assuming an exponential temperature dependence with $Q_{10} = 2.6$ (cf. Zinkler, 1966) between +18 and +3°C and

Table 14. The relationship between body length ($L$) and body dry weight ($W$) of different Collembola species. The relationship is of the form $\log W = \log a + b \log L$, where $L$ is given in mm and $W$ in $\mu$g. The point of intersection is given for species with different equations for adults and juveniles.
(x) = body length excluding head

| Species | | Stage | Intersection (mm) | log $a$ | $b$ | Reference |
|---|---|---|---|---|---|---|
| *Hypogastrura* cf. *manubrialis* | (1) | juv+ad | | 0.99 | 2.55 | Tanaka (1970a) |
| *Neanura* sp. | | juv+ad | | 1.03 | 2.24 | " |
| *Onychiurus armatus* s.l. | (2) | juv | 0.98 | 0.746 | 2.532 | Petersen (1975) |
| " | | ad | | 0.748 | 2.769 | " |
| *Tullbergia krausbaueri* s.l. | (3) | juv+ad | | 0.504 | 2.502 | " |
| *Folsomia quadrioculata* s.l. | (4) | juv | 0.57 | 0.662 | 2.439 | " |
| " | (4) | ad | | 0.750 | 2.799 | " |
| *Isotomiella minor* | | juv | 0.50 | 0.662 | 2.439 | " |
| " | | ad | | 0.796 | 2.881 | " |
| *Isotoma notabilis* | (5) | juv | 0.57 | 0.675 | 2.183 | " |
| " | (5) | ad | | 0.928 | 3.223 | " |
| Entomobryidae sp. | (6) | juv+ad | | 0.83 | 2.50 | Tanaka (1970a) |
| *Lepidocyrtus lignorum* | (x) (7) | juv+ad | | 1.154 | 2.708 | Petersen (1975) |
| *Tomocerus flavescens* | | juv+ad | | 0.964 | 2.744 | " |
| *Megalothorax minimus* | (x) | juv+ad | | 1.602 | 2.113 | " |
| *Sminthurinus aureus/ flammeolus* | (x) (8) | juv+ad | | 2.079 | 3.627 | " |
| *Dicyrtoma minuta* s.l. | (x) | juv | 0.86 | 1.501 | 2.280 | " |
| " | (x) | ad | | 1.598 | 3.796 | " |

(1) used for *H. denticulata, Friesea mirabilis* and *Pseudachorutes dubius*
(2) also used for *Willemia anophthalma* and *Anurida* spp.
(3) also used for *T. quadrispina*
(4) used for *Folsomia* spp. and *Proisotoma minuta*
(5) also used for *I. viridis*
(6) used for *Entomobrya nivalis* and *Pseudosinella alba*
(7) also used for *L. cyaneus*
(8) used for *Sminthurides pumilis, Sminthurinus niger, Bourletiella* cf. *repanda, Sminthurus nigromaculatus* and juvenile Sminthuridae spp.

Table 15. Oxygen consumption rates of Collembola. The rates are, if necessary adjusted to +18°C by assuming a $Q_{10}$ = 2 above +18°C and $Q_{10}$ = 2.6 below +18°C. (x) denotes an approximate mean of a weight range.

| Species | Live wt ($\mu$g) | $mm^3 O_2$ $g^{-1}$ $h^{-1}$ | $mm^3 O_2$ $ind^{-1}$ $h^{-1}$ | Temp. (°C) | $mm^3$ $O_2$ $ind^{-1}$ $h^{-1}$ at+18°C | Reference |
|---|---|---|---|---|---|---|
| *Hypogastrura assimilis* | 140 | 1090 | 0.153 | 20 | 0.133 | Byzova (1973) |
| *H. assimilis* | 150 | 1053 | 0.158 | 20 | 0.138 | " |
| *Ceratophysella armata* | 50 | 1700 | 0.085 | 20 | 0.074 | " |
| *Neanura muscorum* | 325 (x) | 195 | 0.063 | 18 | 0.063 | Zinkler (1966) |
| *Tetrodontophora bielanensis* | 6610 | 165 | 1.091 | 18 | 1.091 | " |
| *Onychiurus fimatus* | 115 (x) | 681 | 0.078 | 18 | 0.078 | " |
| *O. armatus* | 130 (x) | 630 | 0.082 | 18 | 0.082 | " |
| *O. procampatus* | 10 | | 0.010 | 15 | 0.013 | Healey (1967a) |
| *O. procampatus* | 100 | | 0.032 | 15 | 0.043 | " |
| *Onychiurus* sp. | 8 | | 0.006 | 18 | 0.006 | Tanaka (1970b) |
| *O.* sp. | 80 | | 0.034 | 18 | 0.034 | " |
| *Folsomia quadrioculata* | 3 | 1830 | 0.0055 | 15 | 0.007 | Harding & Stuttard (1974) |
| *F. quadrioculata* | 30 | 615 | 0.019 | 15 | 0.025 | " |
| *F. quadrioculata* | 40 | 800 | 0.032 | 16 | 0.039 | Berthet (1964) |
| *Proisotoma minuta* | 11 | 1040 | 0.011 | 20 | 0.010 | Byzova (1973) |
| *Isotomiella minor* | 7 | 1500 | 0.011 | 20 | 0.009 | " |
| *Isotoma notabilis* | 3 | 2470 | 0.0074 | 15 | 0.010 | Harding & Stuttard (1974) |
| *I. notabilis* | 15 | 1345 | 0.020 | 15 | 0.027 | " |
| *I. viridis* | 718 | 545 | 0.391 | 18 | 0.398 | Zinkler (1966) |
| *I. trispinata* | 10 | | 0.013 | 18 | 0.013 | Tanaka (1970b) |
| *I. trispinata* | 80 | | 0.080 | 18 | 0.080 | " |
| *Orchesella flavescens* | 1830 | 527 | 0.965 | 20 | 0.840 | Schaller & Zinkler (1963) |
| *O. cincta* | 1340 | 413 | 0.553 | 18 | 0.553 | Zinkler (1966) |
| *O. villosa* | 2900 | 279 | 0.810 | 22 | 0.614 | Ruppel (1953) |
| *Tomocerus longicornis* | 3600 (x) | 266 | 0.958 | 18 | 0.958 | Zinkler (1966) |
| *T. vulgaris* | 1620 | 365 | 0.591 | 18 | 0.591 | " |
| *Sminthurus viridis* | 2200 (x) | 549 | 1.208 | 18 | 1.208 | " |
| *S. fuscus* | 2900 | 491 | 1.424 | 18 | 1.424 | " |
| *Dicyrtoma minuta* | 590 (x) | 147 | 0.087 | 8 | 0.226 | " |

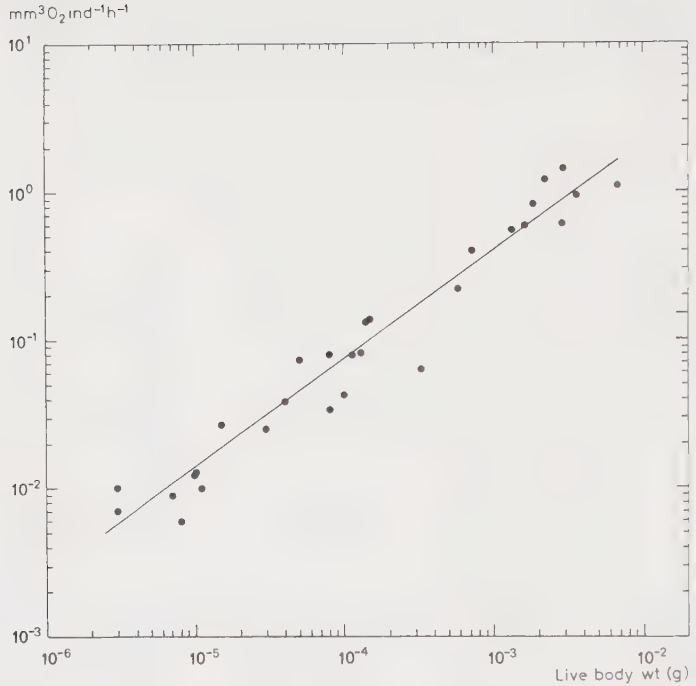


**Figure 14.** The relationship between live body weight ($W$) and oxygen consumption rate ($Q$) at +18°C for 22 different Collembola species based on 29 determinations (see Table 15). The equation of the regression line is log $Q$ = log 63 + 0.73 log $W$.

$Q_{10}$ = 3.6 between +3 and −2°C. The latter value is a mean of $Q_{10}$ = 4.18 for *Isotoma saltans* (Nic.) and $Q_{10}$ = 3.05 for *I. hiemalis* Schött according to Zinkler (*op. cit.*).

The live body weights were obtained from the dry weights by using live weight/dry weight ratios given by Petersen (1975), namely, 2.71 for *Tullbergia krausbaueri* (Börn.), 2.81 for *Folsomia quadrioculata* (Tullb.), 2.81 for *Isotomiella minor* (Schäff.), 2.56 for *Isotoma notabilis* Schäff., 3.50 for *Lepidocyrtus lignorum/lanuginosus*, 3.22 for *Pseudosinella alba* (Packard) and 4.08 for *Tomocerus flavescens* (Tullb.). The value for *L. lignorum* (Fabr.) was also used for *L. cyaneus* Tullb. in this study. The live body weights of other species were obtained from the ratios given by Edwards (1967), who estimated the average dry matter percentages at 36.6 for Hypogastruridae (Poduridae), 28.8. for Onychiuridae, 27.9 for Isotomidae, 31.1 for Entomobryidae and 35.8 for Sminthuridae.

Since the body lengths were always measured to the nearest 0.02 mm, the corresponding weight classes could be very numerous, for example 137 weight classes for *Isotoma viridis* Bourl., which had a range of length classes of 0.46–3.20 mm. The oxygen consumption rates were calculated separately for each weight (or length) class of a species. An example of the calculations of abundance, biomass and oxygen consumption rates is given in Table 16, which shows the length class data and the corresponding weights and oxygen consumption rates for *Folsomia quadrioculata* on one sampling occasion. This type of primary data was used for calculating population estimates and oxygen consumption rates at other samplings and for the other 29 Collembola species.

Table 16. The number of *Folsomia quadrioculata* per soil core and length class on 15 June 1971. The corresponding dry body weight, live body weight and oxygen consumption rate at +18°C are given for each length class. Soil core surface area = 10.8 $cm^2$, soil core depth = = 20 cm, n = 15.

| Length (mm) | Dry wt (µg) | Live wt (µg) | $mm^3$ $O_2$ $ind^{-1}$ $h^{-1}$ (x 1000) | Soil core no.: 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.26 | 0.17 | 0.48 | 1.54 | | | | | | 1 | | | | | | | | | |
| 0.28 | 0.21 | 0.58 | 1.76 | | | | | | | | | | | | | | 1 | 1 |
| 0.30 | 0.24 | 0.69 | 1.99 | | | 1 | | 4 | | | | 2 | | | | | 1 | |
| 0.32 | 0.29 | 0.80 | 2.23 | | | 1 | | | 1 | 1 | | 3 | 3 | | 1 | | 4 | |
| 0.34 | 0.33 | 0.93 | 2.49 | | | | 1 | 6 | 2 | 4 | 1 | 4 | 2 | | | | 3 | 1 |
| 0.36 | 0.38 | 1.07 | 2.75 | | 3 | | 5 | 8 | 10 | 2 | | 8 | 6 | | 2 | | 4 | 3 |
| 0.38 | 0.43 | 1.22 | 3.04 | | | | | 2 | 3 | | | 3 | 1 | | | | 3 | 1 |
| 0.40 | 0.49 | 1.38 | 3.32 | | | | | | 1 | | | | | | | | | |
| 0.42 | 0.55 | 1.55 | 3.62 | | | | | 1 | 1 | | | | | | | | 1 | 2 |
| 0.44 | 0.62 | 1.74 | 3.94 | 1 | | | | | 2 | | | 1 | | | | | | 1 |
| 0.46 | 0.69 | 1.94 | 4.26 | | 2 | | | 1 | | 1 | 1 | 1 | | | | | | |
| 0.48 | 0.77 | 2.15 | 4.60 | | | | | | | | | 2 | | | 1 | | | 1 |
| 0.50 | 0.85 | 2.38 | 4.95 | | 1 | 1 | | 1 | | | | | | | | | | |
| 0.52 | 0.93 | 2.62 | 5.30 | | | | | | | | | | | | | | 1 | |
| 0.54 | 1.02 | 2.87 | 5.67 | | | | | | | | | | | 1 | | | | |
| 0.56 | 1.12 | 3.14 | 6.05 | 1 | | | | | | | | | | | | 1 | | |
| 0.58 | 1.22 | 3.44 | 6.47 | | 2 | 1 | | | 1 | | | | | | | | | |
| 0.60 | 1.35 | 3.79 | 6.94 | 1 | 1 | | | | | | | 1 | | | | | | |
| 0.62 | 1.48 | 4.15 | 7.41 | | 1 | | | | 1 | | | | | | | | | |
| 0.64 | 1.61 | 4.53 | 7.92 | | | 1 | | 1 | | | | | | | | | | |
| 0.66 | 1.76 | 4.94 | 8.42 | | | | | 1 | | | | | | | | | | |
| 0.68 | 1.91 | 5.37 | 8.96 | 1 | | | 1 | | | | | | | | | | 1 | |
| 0.70 | 2.07 | 5.82 | 9.50 | 1 | | 2 | | | | | | | | | | 1 | | |
| 0.72 | 2.24 | 6.30 | 10.07 | | | | | | 1 | | | 1 | 1 | | | | | |
| 0.74 | 2.42 | 6.80 | 10.65 | | 1 | | | | 1 | | | | | | | | 1 | |
| 0.76 | 2.61 | 7.33 | 11.24 | | | | | | 1 | | | 1 | 1 | | | | | |
| 0.78 | 2.81 | 7.88 | 11.85 | 1 | | | | | | 1 | | 2 | | | | | | |
| 0.80 | 3.01 | 8.46 | 12.48 | | 1 | 1 | | | | | | 1 | | 1 | | 1 | 1 | 1 |
| 0.82 | 3.23 | 9.07 | 13.13 | | | | | | | | | 5 | | | | 1 | | |
| 0.84 | 3.45 | 9.70 | 13.79 | | | | | | 2 | | | 1 | | | | | | |
| 0.86 | 3.69 | 10.36 | 14.47 | | | | | | 1 | | | 1 | | | | | | |
| 0.88 | 3.93 | 11.05 | 15.17 | | 1 | | | | 1 | 1 | | 1 | | | | | | |
| 0.90 | 4.19 | 11.76 | 15.88 | | | | | | | | | | | | | | | |
| 0.92 | 4.45 | 12.51 | 16.61 | | | | | 1 | | | | | 1 | | | | | |
| 0.94 | 4.73 | 13.29 | 17.35 | | | | | | | | | | | | | | | |
| 0.96 | 5.02 | 14.10 | 18.13 | | | | | | | | | 2 | | | | | | |
| 0.98 | 5.31 | 14.93 | 18.90 | | | | | | | | | | | | | | | |
| 1.00 | 5.62 | 15.80 | 19.70 | | | | | | | | | | | | | | | |
| . | | | | | | | | | | | | | | | | | | |
| . | | | | | | | | | | | | | | | | | | |
| 1.12 | 7.72 | 21.70 | 24.83 | 1 | | | | | | | | | | | | | | |
| . | | | | | | | | | | | | | | | | | | |
| . | | | | | | | | | | | | | | | | | | |
| 1.34 | 12.76 | 35.85 | 35.82 | | | 1 | | | | | | | | | | | | |
| 1.36 | 13.30 | 37.37 | 36.92 | | | | | | | | | | | | | | | |
| 1.38 | 13.85 | 38.92 | 38.04 | | 1 | | | | | | | | | | | | | |
| no./soil core | | | | 7 | 14 | 9 | 7 | 26 | 30 | 10 | 2 | 40 | 15 | 2 | 4 | 4 | 21 | 11 |
| µg dry wt/soil core | | | | 18 | 32 | 24 | 4 | 17 | 33 | 10 | 1 | 62 | 14 | 4 | 2 | 9 | 14 | 8 |
| $mm^3$ $O_2$ $h^{-1}$ (x 100)/soil core | | | | 7 | 13 | 9 | 3 | 10 | 16 | 5 | 1 | 28 | 7 | 2 | 1 | 4 | 8 | 4 |

## Results

### Species composition

Thirty-two species were observed at Spikbole. Most of them were found in the soil samples, but *Hypogastrura socialis* (Uzel) and *Isotoma violacea* Tullb. were only occasionally observed on top of the snow during mild February days in 1972, and were not found in the randomized soil cores. All species observed are listed in Appendix 2. The taxonomy is mainly based on Gisin (1960), and thus *Tullbergia krausbaueri* was considered as one species, although it is probably a group of species (Rusek, 1971). *Folsomia quadrioculata* (Tullb.) and *Onychiurus armatus* (Tullb.) were only identified as s.l. forms according to Bödvarsson (1970), but at least *O. armatus* s.l. consisted of more than one species sensu Gisin (*op. cit.*). The separation of *Folsomia fimetaria* (L.), *F. litsteri* Bagn. and *F. bisetosa* Gisin was sometimes complicated owing to overlapping characters. Therefore these species were treated collectively as *F. fimetaria* coll. The sminthurid species were difficult to determine as juveniles, and have been pooled in the tables.

### Vertical distribution

The microarthropod soil cores were always taken down to a depth of 20 cm during the "summer" period, but the cores were mostly compressed to about 16 cm in the corer because of the loose peat soil. When the soil cores were divided into 2 cm sub-cores in the laboratory, each 2 cm sub-core, consequently consisted of about 2.5 cm of the undisturbed soil profile. The vertical distribution of total Collembola and some of the most abundant species in the litter (L) layer and soil is shown in Fig. 15, which is corrected for the vertical compression. This was not necessary during the winter when the soil was frozen.

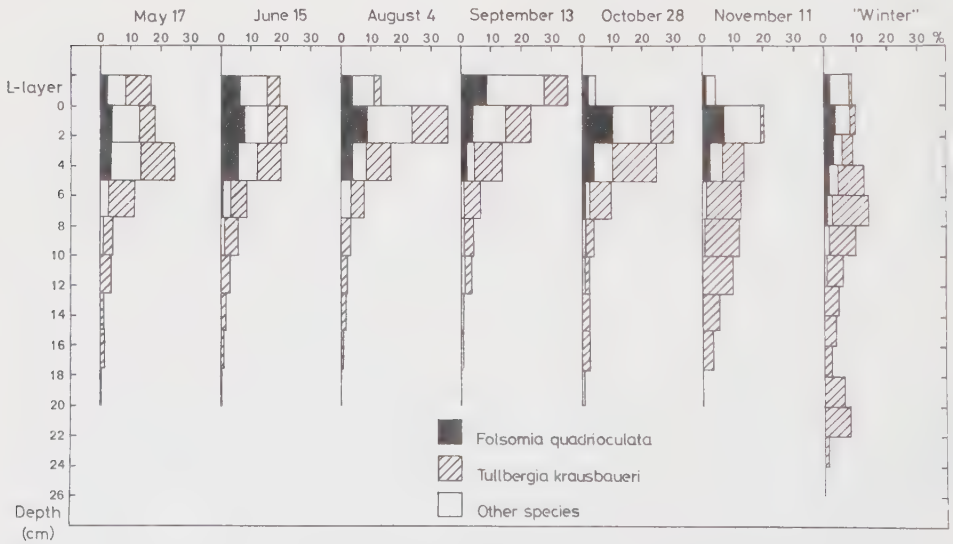


**Figure 15.** The vertical distribution of Collembola in 1971–72. The numbers of collembolans per 2 cm vertical layers are expressed as percentages of the total number on each sampling occasion. L = litter.

More than 70 % of the total number of Collembola were found in the litter and the top 5 cm of the peat soil during May to October. In November the proportion was 47 % and in the "winter" only 35 %. The percentage of total Collembola above the 10 cm level was estimated at 91 in May, 90 in June, 93 in August, 95 in September, 91 in October, 77 in November and 67 during the "winter". The difference in vertical distribution between September and "winter" was significant ($P < 0.01$).

*Pseudachorutes dubius* Krausb., *Isotoma viridis* and adults of the three species *Entomobrya nivalis* (L.), *Lepidocyrtus cyaneus* and *L. lignorum* were found in the litter and in the upper 2 cm of the peat soil. *Folsomia quadrioculata* and *Isotoma notabilis* usually had a maximum at a depth of 0–4 cm. *F. quadrioculata* was seldom found below the 8 cm level, while *I. notabilis* could occur somewhat deeper during the "winter". *Willemia anophthalma* Börn., *Friesea mirabilis* (Tullb.), juvenile *E. nivalis*, juvenile *L. cyaneus* and *Megalothorax minimus* Willem were sometimes observed down to about 10 cm. *Isotomiella minor* and *Folsomia fimetaria* coll. usually had the greatest density between 2 and 6 cm, but occurred frequently down to about 10 cm and were occasionally found deeper. *Tullbergia krausbaueri* and *T. quadrispina* (Börn.) appeared to have the most extreme vertical distribution of the collembolans at Spikbole. *T. krausbaueri* was most responsible for the changes in vertical distribution of total Collembola during the year because of its numerical dominance. During May to October the greatest number of *T. krausbaueri* were found at about the 4 cm level, except for the August sampling when they were shallower, but in November the median depth had increased to 7.5 -10 cm and during the "winter" to 8–10 cm. Two density maxima were observed for *T. krausbaueri* during the "winter". The shallower maximum was at about 6–8 cm, and the deeper maximum at 18–22 cm. During the "winter" about 92 % of all Collembola found below 10 cm belonged to *T. krausbaueri.*

*Isotoma viridis, Entomobrya nivalis, Lepidocyrtus cyaneus* and *L. lignorum* were the only collembolans found in the snow samples. As an average 14 % of the total number of *I. viridis*, 19 % of *E. nivalis*, 25 % of *L. lignorum* but only 0.3 % of *L. cyaneus* were found on or in the snow on those occasions when the snow cover was more than 5 cm deep.

Large *L. cyaneus* seemed to be estimated with the same efficiency according to the high gradient canister extraction as in the Tullgren funnel extraction, but the study of the vertical distribution revealed that *L. cyaneus* juveniles occurred at greater depths than those taken with the macroarthropod sampler. It was therefore decided to use the high gradient canister data for calculating the abundance and biomass of this species. Small *E. nivalis* were also found at larger depths, but large specimens on the other hand were probably underestimated in the high gradient canister extractor, since they escaped from the soil cores during extraction. Therefore, the abundance, biomass and respiration of *E. nivalis* was estimated by means of a combination of high gradient canister and Tullgren data. Specimens smaller than 0.80 mm were estimated by means of the former extractor, and specimens of 0.80 mm or larger by means of the latter. The five species, *Pseudachorutes dubius, Isotoma viridis, Lepidocyrtus lignorum, Pseudosinella alba* and *Tomocerus flavescens* were not found deeper than 3 cm, and since even juvenile forms seemed to be sufficiently extracted in the Tullgren funnels, the population estimates of these large species were based wholly on this extraction method, except for May 17 and August 4, when no soil cores were taken for Tullgren extraction.

**Abundance**

The abundances of the different Collembola species during the main study period, including the complementary August sampling, are presented in Table 17. Since no Tullgren funnel extractions (T) were made on May 17 or August 4, Macfadyen high gradient canister extractions (M) had to be used on these dates to complete the T-values for the other dates. The combined abundance estimates are indicated by M+T in Table 17. The number of total Collembola based on M-data only is given for comparison.

The most abundant species on all sampling occasions was *Tullbergia krausbaueri*, which accounted for about 50 % of the total number of Collembola during the six "summer" samplings and about 65 % during the "winter" sampling. The "winter" density was 130 000 (*s.e.* = 32 000) specimens $m^{-2}$, which was significantly higher ($P < 0.05$) than that of the "summer" with 33 000 (*s.e.* = 5200) $m^{-2}$. Other species with fairly high abundances were *Folsomia quadrioculata* with an annual mean of 14 600 (*s.e.* = 1100), *Isotoma notabilis* with 11 400 (*s.e.* = 2100) and *Isotomiella minor* with 5500 (*s.e.* = 1300) individuals $m^{-2}$. The abundance of total Collembola ranged from about 49 000 to 95 000 $m^{-2}$ during the "summer". During the "winter" it was estimated at 195 000 (*s.e.* = 33 000) $m^{-2}$. The annual mean abundance was estimated at 109 000 (*s.e.* = 12 000) collembolans $m^{-2}$.

For some species the fluctuations in abundance could be correlated with changes in the size composition. *F. quadrioculata* increased in numbers from the May to the June sampling, which was obviously caused by frequent hatching (Fig. 16). A less conspicuous hatching period may have occurred before the September sampling. The size distributions in August and during the "winter" were dominated by adults (approximately > 0.60 mm) and large juveniles.

The high abundances of *I. minor* in May and August coincided with a large number of small juveniles. The May sampling yielded the highest density of newly hatched individuals (0.20–0.26 mm), while adults (about 0.50 0.70 mm) and large juveniles dominated during the autumn and winter (Fig. 17).

*I. notabilis* had a great number of juveniles in the smaller size classes (0.28–0.40 mm) on all sampling occasions except for the "winter", when adults (about 0.50–0.80 mm) and large juveniles were dominant (Fig. 18).

The relatively high abundances of *T. krausbaueri* in August and September coincided with a greater proportion of small individuals than on the other sampling occasions, but the form of the frequency distribution figures did not differ much during the year (Fig. 19).

The increase in number of *E. nivalis* between the May and June samplings was obviously caused by hatching, since the June population consisted of a great proportion of small juveniles (0.40–0.50 mm) which were not found in May (Fig. 20). The hatching seemed to be protracted over a longer period, since many small juveniles were also recorded in August. No larger juveniles but many adults were observed in June, which indicated that the adults belonged to the preceding year's generation. The number of juveniles successively decreased during the autumn and winter. The same tendency, although displaced in time, was found for *L. cyaneus*, which had only adults in June and many small juveniles in August (Fig. 21).

During the "winter" most populations seemed to consist of many large juveniles and adults and relatively few small juveniles. Small juveniles dominated only among Sminthuridae during that season.

Table 17. Abundance (no. $m^{-2}$) of Collembola in 1971–72. The August values are not used for calculating "summer" and annual means. Standard error is given within parentheses below the corresponding mean value.
M = Macfadyen high gradient canister extraction
T = Tullgren funnel extraction

| | | May 17 | June 15 | Aug 4 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|---|
| *Hypogastrura denticulata* | (M) | 0 | 860 (410) | 0 | 370 (260) | 310 (150) | 120 (120) | 330 (150) | 280 (150) | 320 (110) |
| *Willemia anophthalma* | (M) | 0 | 250 (170) | 62 (62) | 0 | 120 (120) | 120 (84) | 99 (47) | 160 (99) | 120 (45) |
| *Friesea mirabilis* | (M) | 190 (190) | 190 (99) | 62 (62) | 430 (270) | 190 (99) | 430 (430) | 280 (61) | 0 | 190 (41) |
| *Pseudachorutes dubius* | (M+T) | 0 | 120 (67) | 120 (85) | 250 (60) | 360 (120) | 190 (37) | 180 (61) | 270 (100) | 210 (53) |
| *Anurida pygmaea* | (M) | 62 (62) | 1 900 (890) | 860 (310) | 990 (500) | 190 (99) | 490 (270) | 730 (340) | 1 800 (840) | 1 100 (360) |
| *A. ellipsoides* | (M) | 62 (62) | 0 | 0 | 0 | 0 | 0 | 12 (12) | 0 | 8.2 (8.2) |
| *A. granaria* | (M) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 130 (72) | 42 (24) |
| *Neanura muscorum* | (M) | 0 | 0 | 0 | 0 | 0 | 190 (140) | 37 (37) | 220 (190) | 98 (68) |
| *Onychiurus armatus* | (M) | 62 (62) | 190 (140) | 0 | 0 | 0 | 120 (120) | 74 (36) | 370 (220) | 170 (77) |
| *Tullbergia krausbaueri* | (M) | 29 000 (4 900) | 20 700 (3 000) | 41 700 (7 600) | 40 700 (10 500) | 26 000 (5 700) | 48 800 (12 200) | 33 000 (5 200) | 130 000 (31 800) | 65 000 (11 200) |
| *T. quadrispina* | (M) | 1 100 (390) | 680 (360) | 62 (62) | 0 | 190 (99) | 430 (240) | 480 (200) | 860 (340) | 610 (170) |
| *Folsomia quadrioculata* | (M) | 7 600 (1 100) | 12 500 (2 700) | 19 000 (4 400) | 11 400 (2 200) | 9 800 (2 900) | 9 800 (2 700) | 10 200 (830) | 23 500 (2 800) | 14 600 (1 100) |
| *F. fimetaria* coll. | (M) | 620 (250) | 370 (180) | 3 100 (1 200) | 2 400 (960) | 1 800 (1 100) | 2 700 (1 400) | 1 600 (470) | 5 200 (1 700) | 2 800 (630) |
| *Isotomiella minor* | (M) | 8 000 (3 600) | 2 300 (620) | 8 500 (2 600) | 2 600 (1 000) | 1 600 (740) | 3 100 (1 200) | 3 500 (1 200) | 9 500 (2 900) | 5 500 (1 300) |
| *Proisotoma minuta* | (M) | 0 | 0 | 0 | 0 | 0 | 120 (84) | 25 (25) | 0 | 16 (16) |
| *Isotoma notabilis* | (M) | 7 700 (1 500) | 4 600 (1 500) | 13 000 (2 700) | 17 700 (3 200) | 9 800 (2 200) | 12 300 (3 700) | 10 400 (2 300) | 13 600 (4 200) | 11 400 (2 100) |
| *I. viridis* | (M+T) | 620 (150) | 150 (70) | 620 (180) | 830 (120) | 710 (200) | 800 (220) | 620 (130) | 490 (87) | 580 (88) |
| *Entomobrya nivalis* | (M+T) | 860 (320) | 3 800 (850) | 3 000 (680) | 3 100 (1 300) | 1 200 (380) | 1 500 (490) | 2 100 (570) | 1 100 (320) | 1 800 (400) |
| *Lepidocyrtus cyaneus* | (M) | 1 800 (540) | 490 (200) | 3 100 (730) | 2 000 (570) | 990 (270) | 860 (230) | 1 200 (300) | 3 500 (2 300) | 2 000 (770) |
| *L. lignorum* | (M+T) | 0 | 48 (33) | 62 (62) | 180 (86) | 560 (270) | 290 (150) | 210 (100) | 240 (58) | 220 (70) |
| *Pseudosinella alba* | (M+T) | 0 | 0 | 0 | 16 (16) | 0 | 0 | 3.2 (3.2) | 0 | 2.1 (2.1) |
| *Tomocerus flavescens* | (M+T) | 0 | 0 | 0 | 0 | 0 | 5.3 (5.3) | 1.1 (1.1) | 0 | 0.7 (0.7) |
| *Megalothorax minimus* | (M) | 120 (84) | 0 | 190 (99) | 0 | 62 (62) | 190 (140) | 74 (36) | 190 (75) | 110 (35) |
| Sminthuridae spp. | (M) | 930 (300) | 190 (99) | 430 (130) | 250 (150) | 620 (370) | 560 (310) | 510 (140) | 3 100 (1 200) | 1 400 (400) |
| Collembola, total | (M) | 58 700 (6 100) | 48 600 (5 400) | 94 300 (11 800) | 82 600 (13 400) | 53 100 (7 500) | 82 200 (13 800) | 65 000 (7 300) | 194 200 (32 700) | 108 100 (11 900) |
| Collembola, total | (M+T) | 58 700 | 49 200 | 94 300 | 83 200 | 54 400 | 83 200 | 65 800 (7 300) | 194 500 (32 500) | 108 700 (11 900) |

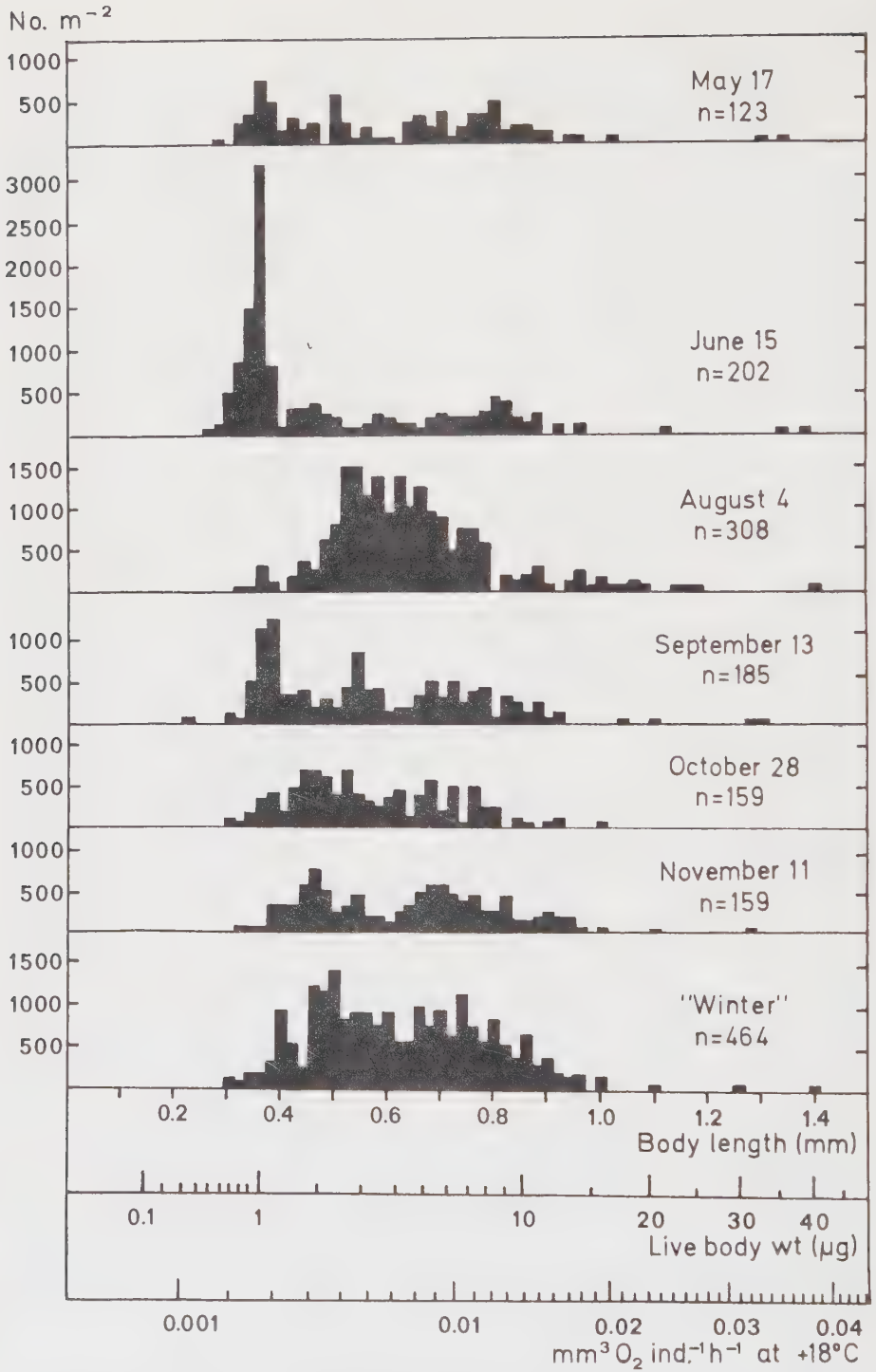


**Figure 16.** The size class distribution of *Folsomia quadrioculata* in 1971–72. Each 0.02 mm body length class is given per $m^2$. The corresponding body weights and oxygen consumption rates are indicated.

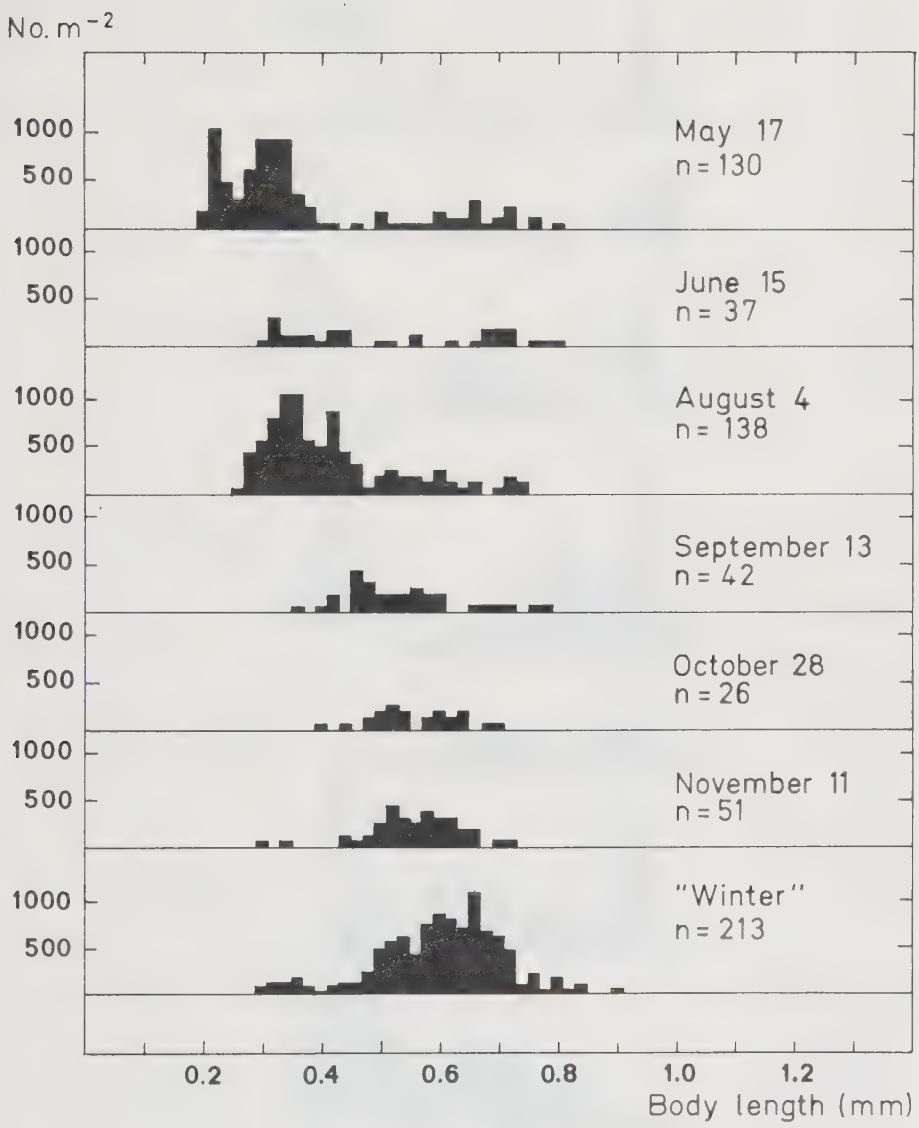


**Figure 17.** The size class distribution of *Isotomiella minor* in 1971–72. Each 0.02 mm body length class is given per $m^2$.

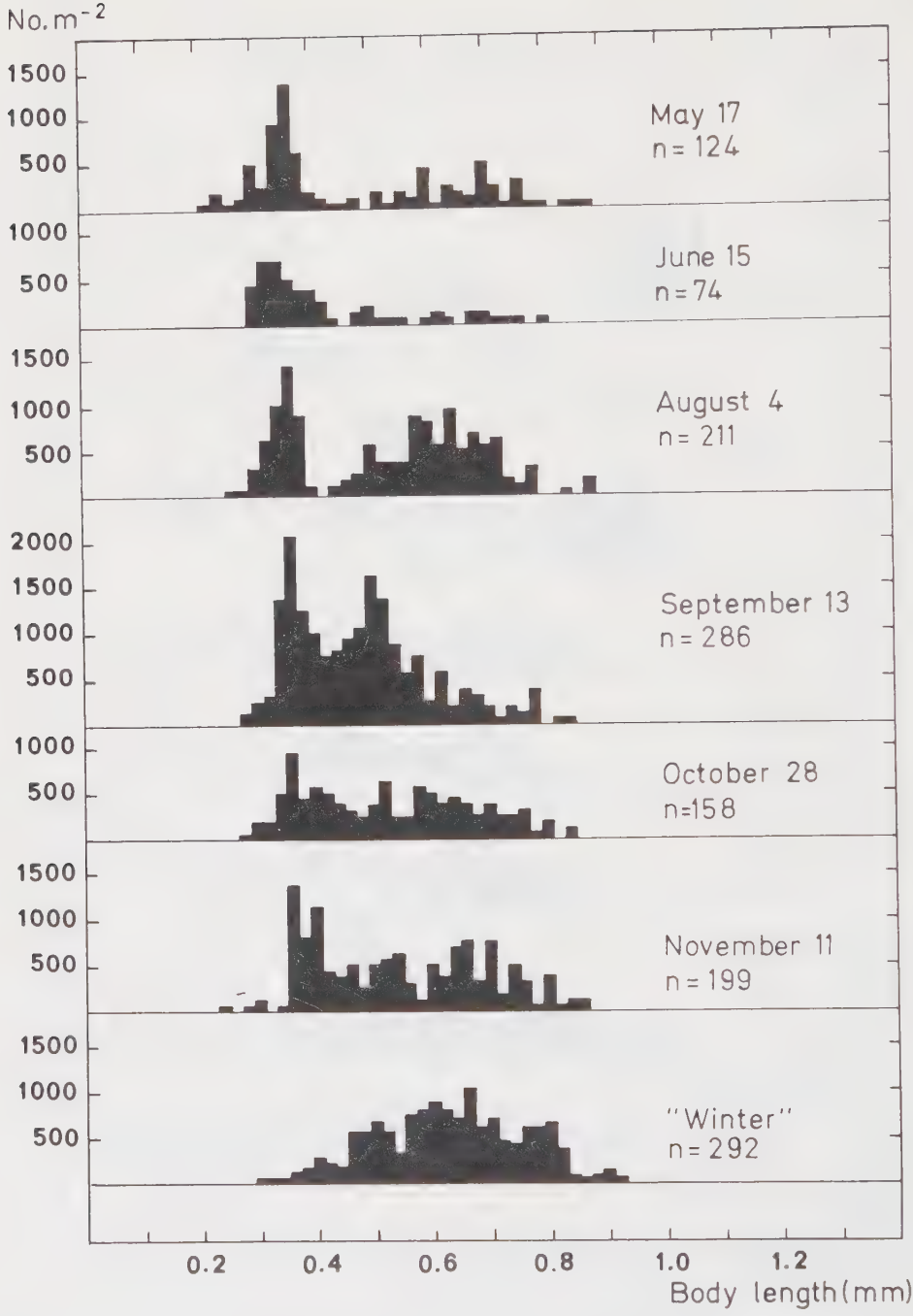


Figure 18. The size class distribution of *Isotoma notabilis* in 1971–72. Each 0.02 mm body length class is given per $m^2$.

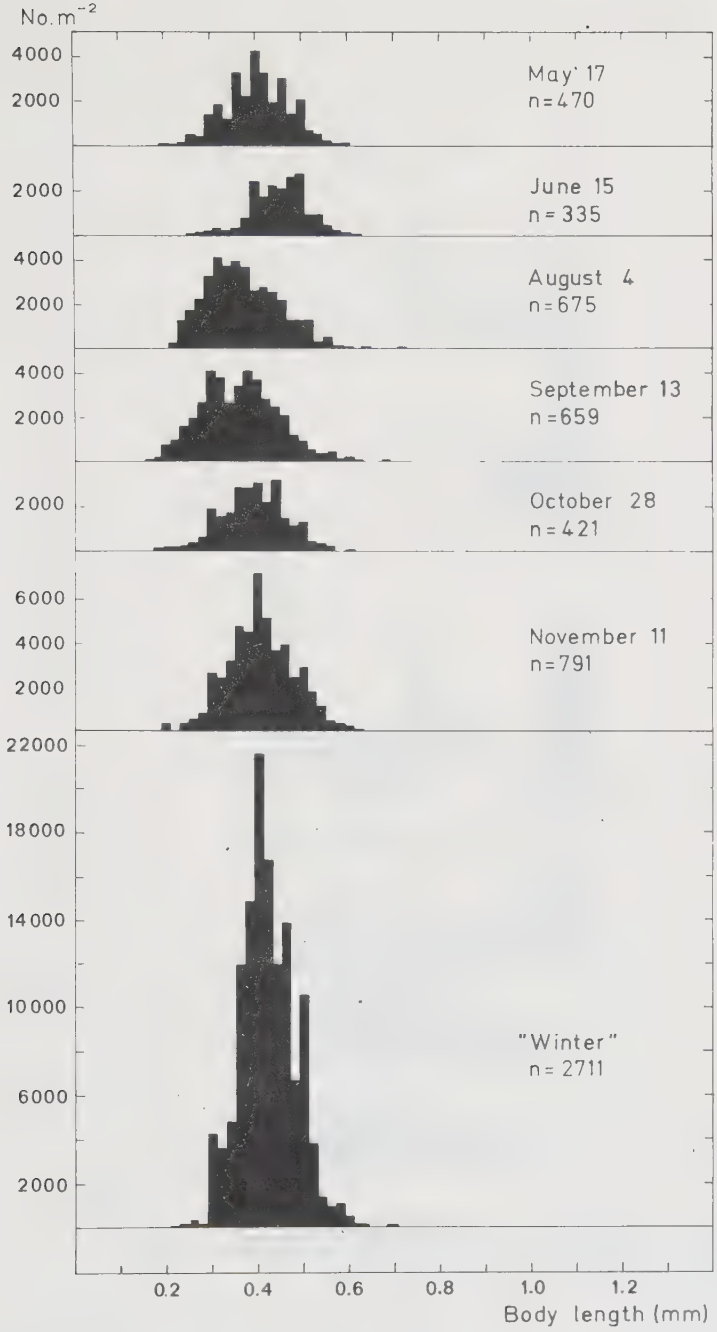


**Figure 19.** The size class distribution of *Tullbergia krausbaueri* in 1971–72. Each 0.02 mm body length class is given per $m^2$.

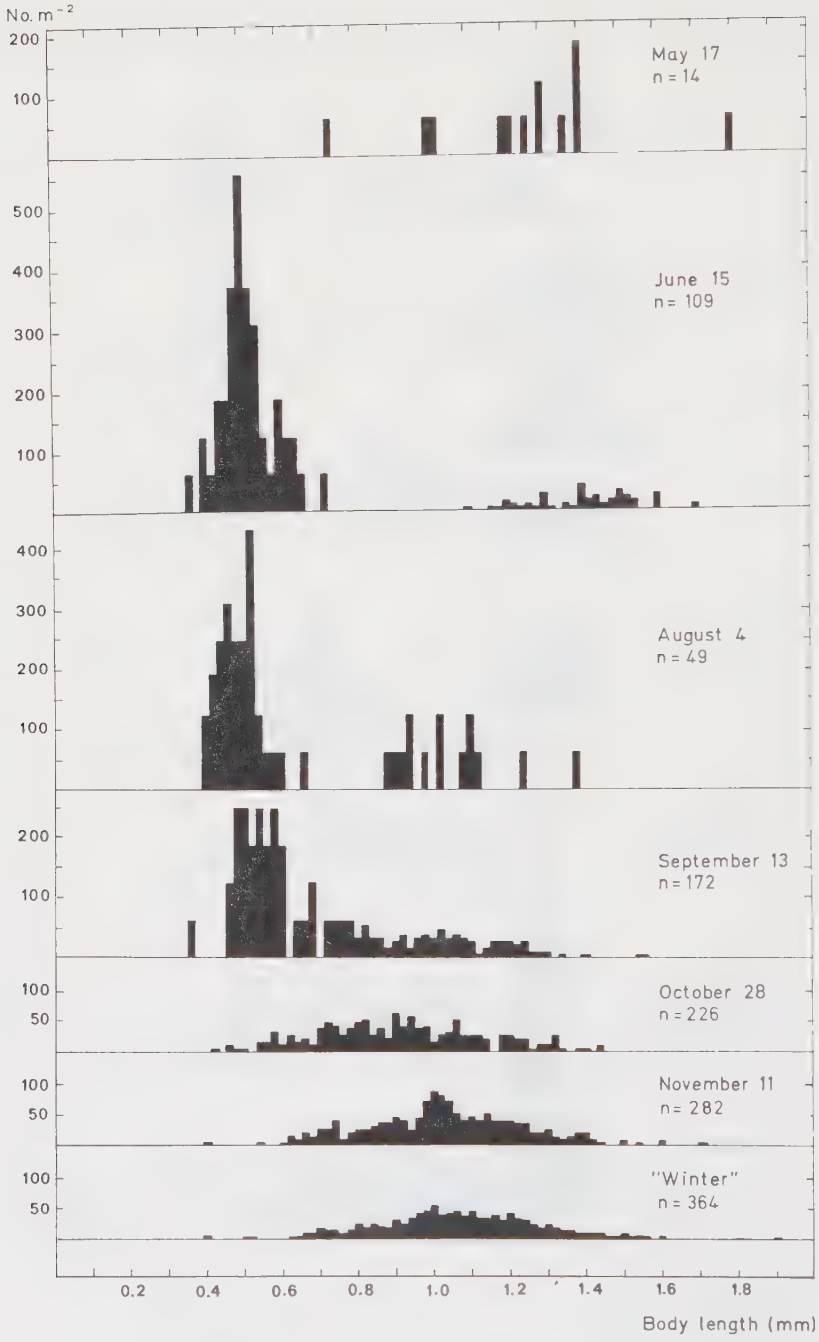


**Figure 20.** The size class distribution of *Entomobrya nivalis* in 1971–72 based on two kinds of sample units (see text). Each 0.02 mm body length class is given per $m^2$.

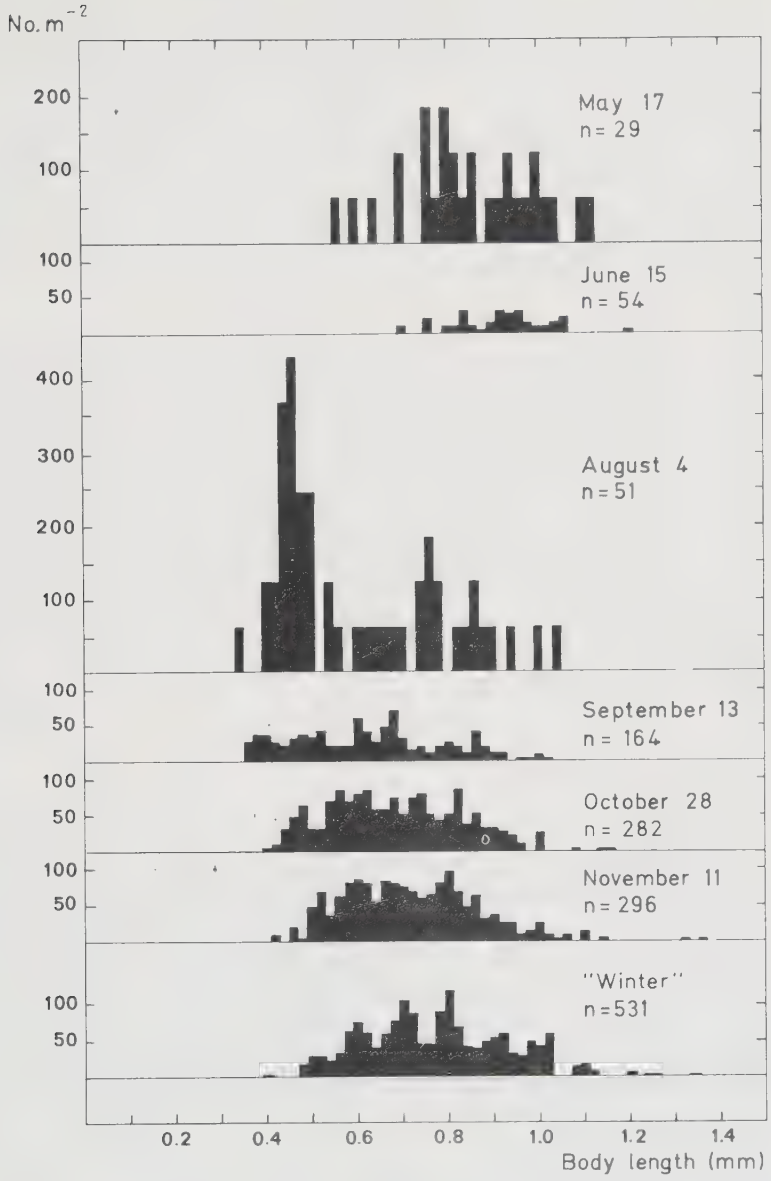


**Figure 21.** The size class distribution of *Lepidocyrtus cyaneus* in 1971–72. The distributions in May and August are based on a sample unit of 10.8 $cm^2$ surface area, while the others are based on a surface area of 188 $cm^2$. Each 0.02 mm body length class is given per $m^2$.

### Biomass

The biomasses of the Collembola species and the total Collembola community are given in Table 18. Large and mobile species as *Isotoma viridis* were extracted more efficiently in the Tullgren funnels than in the high gradient canisters. These species had considerable effect on the total Collembola biomass because of their large size, and consequently the total biomass based on both methods (M+T) was larger than the biomass based on high gradient canister extraction (M) alone. The highest mean biomasses per year were estimated for *I. viridis, F. quadrioculata, T. krausbaueri* and *I. notabilis* with 30 (*s.e.* = 6.8), 24 (*s.e.* = 1.6), 24 (*s.e.* = 4.6) and 19 (*s.e.* = 3.8) mg dw $m^{-2}$, respectively. The total Collembola biomass ranged from 69 to 140 mg $m^{-2}$ during the "summer" period, and was estimated at 220 (*s.e.* = 28) mg $m^{-2}$ during the "winter". The annual mean biomass was estimated at 140 (*s.e.* = 13) mg $m^{-2}$.

### Respiration

The oxygen consumption rates $m^{-2}$ of different Collembola species and the whole Collembola community are given in Table 19. The table also shows the annual respiration. *T. krausbaueri* had the highest annual respiration with 1.5 (*s.e.* = 0.21) kcal $m^{-2}$. Other species with relatively high respiration were *F. quadrioculata* with 1.1 (*s.e.* = 0.11), *I. notabilis* with 0.82 (*s.e.* = 0.15) and *I. viridis* with 0.76 (*s.e.* = 0.23) kcal $m^{-2}$ $yr^{-1}$. The oxygen consumption rates of total Collembola varied between 2.4 and 9.7 $cm^3$ $O_2$ $m^{-2}$ $day^{-1}$ on the "summer" samplings. The highest value was obtained in the supplementary August sampling, when the soil temperature was +15°C. The other rates were much lower and of the same magnitude as the "winter" rate. The annual respiration of total Collembola was estimated at 6.1 (*s.e.* = 0.64) kcal $m^{-2}$ $yr^{-1}$.

## Discussion

### Vertical distribution

The vertical distribution of Collembola at Spikbole was concentrated to the uppermost soil layers during the "summer", but was extended to greater depths during the "winter". Seasonal variations in vertical distribution have been recorded by several authors, e.g. Volz (1934), Glasgow (1939), van der Drift (1951), Milne (1962), Hale (1966) and Usher (1970), and appears to be a common feature, at least in temperate habitats. It is often interpreted as caused by vertical migration during periods of adverse conditions in the upper layers of the soil, but it can also be due to differential natality and mortality. Very few specimens during the "winter" were small enough to have been recently hatched, and the size distributions of species occurring at greater depths, e.g. *T. krausbaueri, F. fimetaria* coll. and *I. minor*, did not differ from those at shallower depths. This confirmed the hypothesis of vertical migration.

Low temperatures have been observed to cause vertical migration (Usher, 1970), and the rapid change in vertical distribution of *T. krausbaueri* between October 28 and November 11 was probably initiated by the marked drop in soil temperature which preceded the November sampling (cf. Fig. 8). Healey (1967c) pointed out that where soils have been saturated by rainfall or thaw, and then frozen, arthropods that have not migrated to deeper layers will be inactivated. This is probably what happened to a majority of

Table 18. Biomass (mg dry weight $m^{-2}$) of Collembola in 1971–72. The August values are not used for calculating "summer" and annual means. Standard error is given within parentheses below the corresponding mean value.
M = Macfadyen high gradient canister extraction
T = Tullgren funnel extraction

| | | May 17 | June 15 | Aug 4 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|---|
| *Hypogastrura denticulata* | | 0 | 0.86 (0.41) | 0 | 0.47 (0.26) | 1.69 (1.05) | 0.37 (0.37) | 0.68 (0.29) | 1.25 (0.65) | 0.87 (0.29) |
| *Willemia anophthalma* | | 0 | 0.06 (0.04) | 0.02 (0.02) | 0 | 0.11 (0.11) | 0.08 (0.06) | 0.05 (0.03) | 0.10 (0.08) | 0.07 (0.03) |
| *Friesea mirabilis* | | 0.61 (0.61) | 0.85 (0.46) | 0.04 (0.04) | 0.81 (0.50) | 0.42 (0.29) | 1.09 (1.09) | 0.76 (0.12) | 0 | 0.50 (0.08) |
| *Pseudachorutes dubius* | | 0 | 0.89 (0.48) | 1.44 (1.19) | 0.88 (0.27) | 1.27 (0.45) | 1.21 (0.38) | 0.85 (0.23) | 1.21 (0.46) | 0.97 (0.22) |
| *Anurida pygmaea* | | 0.01 (0.01) | 0.63 (0.28) | 0.66 (0.25) | 0.49 (0.19) | 0.11 (0.07) | 0.37 (0.22) | 0.32 (0.12) | 1.80 (1.10) | 0.81 (0.38) |
| *A. ellipsoides* | | 0.13 (0.13) | 0 | 0 | 0 | 0 | 0 | 0.03 (0.03) | 0 | 0.02 (0.02) |
| *A. granaria* | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.37 (0.22) | 0.12 (0.08) |
| *Neanura muscorum* | | 0 | 0 | 0 | 0 | 0 | 4.55 (4.14) | 0.91 (0.91) | 1.53 (1.24) | 1.12 (0.74) |
| *Onychiurus armatus* | | 1.81 (1.81) | 2.06 (1.90) | 1.35 (0.86) | 0 | 0 | 1.15 (1.15) | 1.00 (0.44) | 4.52 (2.77) | 2.17 (0.97) |
| *Tullbergia krausbaueri* | | 10.33 (1.75) | 9.45 (1.32) | 12.67 (2.30) | 11.22 (2.67) | 8.54 (1.84) | 17.40 (4.17) | 11.39 (1.57) | 50.32 (13.32) | 24.36 (4.56) |
| *T. quadrispina* | | 2.11 (0.71) | 1.37 (0.71) | 0.24 (0.24) | 0 | 0.53 (0.29) | 0.73 (0.41) | 0.95 (0.37) | 1.81 (0.68) | 1.23 (0.34) |
| *Folsomia quadrioculata* | | 13.80 (4.19) | 15.47 (3.83) | 35.23 (8.43) | 17.75 (5.23) | 13.36 (3.52) | 18.71 (5.51) | 15.82 (1.06) | 41.70 (4.30) | 24.45 (1.60) |
| *F. fimetaria* coll. | | 2.19 (0.93) | 1.30 (0.65) | 5.82 (1.98) | 5.29 (1.82) | 2.74 (1.64) | 5.42 (2.68) | 3.39 (0.84) | 14.14 (4.57) | 6.97 (1.62) |
| *Isotomiella minor* | | 4.65 (1.49) | 2.77 (0.73) | 5.47 (1.58) | 2.91 (1.20) | 1.96 (0.80) | 3.86 (1.41) | 3.23 (0.47) | 15.50 (5.90) | 7.32 (1.99) |
| *Proisotoma minuta* | | 0 | 0 | 0 | 0 | 0 | 0.12 (0.08) | 0.02 (0.02) | 0 | 0.02 (0.02) |
| *Isotoma notabilis* | | 9.78 (2.23) | 4.12 (1.38) | 19.59 (4.39) | 19.33 (3.27) | 14.08 (2.86) | 19.44 (4.11) | 13.35 (2.93) | 29.56 (9.69) | 18.75 (3.78) |
| *I. viridis* | | 69.33 (24.97) | 13.53 (6.54) | 19.10 (11.54) | 19.26 (3.07) | 26.84 (5.56) | 38.10 (11.01) | 33.41 (9.88) | 22.89 (3.89) | 29.91 (6.71) |
| *Entomobrya nivalis* | | 11.14 (3.60) | 9.88 (2.71) | 9.24 (3.10) | 9.62 (2.70) | 7.12 (1.69) | 11.74 (4.10) | 9.90 (2.71) | 9.29 (2.55) | 9.70 (1.01) |
| *Lepidocyrtus cyaneus* | | 10.32 (3.71) | 4.35 (1.66) | 8.07 (1.85) | 8.12 (2.22) | 4.19 (1.02) | 3.06 (0.87) | 6.01 (1.38) | 17.99 (10.89) | 10.00 (3.75) |
| *L. lignorum* | | 0 | 0.37 (0.28) | 0.18 (0.18) | 0.77 (0.42) | 2.45 (1.17) | 1.28 (0.65) | 0.98 (0.43) | 1.64 (0.37) | 1.20 (0.31) |
| *Pseudosinella alba* | | 0 | 0 | 0 | 0.04 (0.04) | 0 | 0 | 0.01 (0.01) | 0 | 0.01 (0.01) |
| *Tomocerus flavescens* | | 0 | 0 | 0 | 0 | 0 | 1.19 (1.19) | 0.24 (0.24) | 0 | 0.16 (0.16) |
| *Megalothorax minimus* | | 0.17 (0.13) | 0 | 0.16 (0.09) | 0 | 0.04 (0.04) | 0.13 (0.11) | 0.07 (0.04) | 0.17 (0.12) | 0.10 (0.05) |
| Sminthuridae spp. | | 1.65 (0.75) | 1.09 (0.76) | 0.48 (0.41) | 2.01 (1.93) | 0.82 (0.39) | 0.52 (0.29) | 1.22 (0.28) | 1.92 (0.50) | 1.45 (0.25) |
| Collembola, total | (M) | 138.05 (33.27) | 60.36 (8.31) | 119.74 (17.33) | 87.92 (11.08) | 59.51 (6.61) | 103.07 (11.80) | 89.78 (14.65) | 198.81 (27.99) | 126.12 (13.51) |
| Collembola, total | (M+T) | 138.05 | 69.06 | 119.74 | 98.97 | 86.24 | 130.52 | 104.57 (13.08) | 217.35 (27.11) | 142.16 (12.56) |

Table 19. Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) and the annual respiration (kcal $m^{-2}$) of Collembola in 1971–72. The August values are not used for calculating "summer" and annual mean rates. Standard error is given within parentheses below the corresponding mean value. + denotes a value less than 0.0005.

| | Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) | | | | | | | | | Annual respiration (kcal $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|---|
| | May 17 | June 15 | Aug 4 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual | |
| *Hypogastrura denticulata* | 0 | 0.054 | 0 | 0.021 | 0.039 | 0.007 | 0.024 (0.010) | 0.016 (0.008) | 0.021 (0.008) | 0.037 (0.013) |
| *Willemia anophthalma* | 0 | 0.005 | 0.003 | 0 | 0.004 | 0.002 | 0.002 (0.001) | 0.002 (0.002) | 0.002 (0.001) | 0.004 (0.002) |
| *Friesea mirabilis* | 0.027 | 0.035 | 0.004 | 0.033 | 0.012 | 0.021 | 0.026 (0.005) | 0 | 0.017 (0.003) | 0.030 (0.005) |
| *Pseudachorutes dubius* | 0 | 0.032 | 0.070 | 0.029 | 0.032 | 0.017 | 0.022 (0.007) | 0.015 (0.006) | 0.020 (0.005) | 0.034 (0.008) |
| *Anurida pygmaea* | 0.001 | 0.052 | 0.070 | 0.028 | 0.005 | 0.010 | 0.019 (0.010) | 0.033 (0.019) | 0.024 (0.009) | 0.042 (0.016) |
| *A. ellipsoides* | 0.007 | 0 | 0 | 0 | 0 | 0 | 0.001 (0.001) | 0 | 0.001 (0.001) | 0.002 (0.002) |
| *A. granaria* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.005 (0.003) | 0.002 (0.001) | 0.003 (0.002) |
| *Neanura muscorum* | 0 | 0 | 0 | 0 | 0 | 0.045 | 0.009 (0.009) | 0.017 (0.014) | 0.012 (0.008) | 0.021 (0.014) |
| *Onychiurus armatus* | 0.055 | 0.071 | 0.096 | 0 | 0 | 0.018 | 0.029 (0.015) | 0.051 (0.031) | 0.036 (0.014) | 0.063 (0.025) |
| *Tullbergia krausbaueri* | 0.838 | 0.721 | 1.663 | 0.752 | 0.427 | 0.572 | 0.662 (0.073) | 1.214 (0.315) | 0.846 (0.116) | 1.486 (0.204) |
| *T. quadrispina* | 0.131 | 0.084 | 0.019 | 0 | 0.018 | 0.019 | 0.050 (0.025) | 0.033 (0.013) | 0.045 (0.017) | 0.078 (0.030) |
| *Folsomia quadrioculata* | 0.698 | 0.834 | 2.871 | 0.733 | 0.455 | 0.389 | 0.622 (0.086) | 0.662 (0.069) | 0.635 (0.062) | 1.116 (0.108) |
| *F. fimetaria* coll. | 0.113 | 0.068 | 0.561 | 0.241 | 0.106 | 0.135 | 0.132 (0.030) | 0.240 (0.076) | 0.168 (0.032) | 0.295 (0.057) |
| *Isotomiella minor* | 0.317 | 0.159 | 0.589 | 0.138 | 0.071 | 0.094 | 0.156 (0.044) | 0.258 (0.092) | 0.190 (0.042) | 0.333 (0.074) |
| *Proisotoma minuta* | 0 | 0 | 0 | 0 | 0 | 0.004 | 0.001 (0.001) | 0 | 0.001 (0.001) | 0.001 (0.001) |
| *Isotoma notabilis* | 0.510 | 0.239 | 1.574 | 0.850 | 0.441 | 0.399 | 0.488 (0.101) | 0.421 (0.137) | 0.465 (0.082) | 0.818 (0.143) |
| *I. viridis* | 1.325 | 0.289 | 0.779 | 0.423 | 0.419 | 0.370 | 0.565 (0.192) | 0.170 (0.026) | 0.434 (0.128) | 0.762 (0.225) |
| *Entomobrya nivalis* | 0.388 | 0.434 | 0.690 | 0.352 | 0.182 | 0.189 | 0.309 (0.053) | 0.109 (0.031) | 0.242 (0.037) | 0.426 (0.064) |
| *Lepidocyrtus cyaneus* | 0.476 | 0.180 | 0.685 | 0.319 | 0.126 | 0.065 | 0.233 (0.074) | 0.258 (0.158) | 0.241 (0.072) | 0.424 (0.127) |
| *L. lignorum* | 0 | 0.016 | 0.016 | 0.030 | 0.073 | 0.026 | 0.029 (0.013) | 0.022 (0.005) | 0.026 (0.009) | 0.047 (0.015) |
| *Pseudosinella alba* | 0 | 0 | 0 | 0.002 | 0 | 0 | + | 0 | + | + |
| *Tomocerus flavescens* | 0 | 0 | 0 | 0 | 0 | 0.009 | 0.002 (0.002) | 0 | 0.001 (0.001) | 0.002 (0.002) |
| *Megalothorax minimus* | 0.010 | 0 | 0.016 | 0 | 0.002 | 0.004 | 0.003 (0.002) | 0.003 (0.002) | 0.003 (0.002) | 0.006 (0.003) |
| Sminthuridae spp. | 0.086 | 0.041 | 0.036 | 0.005 | 0.028 | 0.013 | 0.035 (0.015) | 0.041 (0.012) | 0.037 (0.011) | 0.064 (0.018) |
| Collembola, total | 4.982 | 3.314 | 9.742 | 3.956 | 2.440 | 2.408 | 3.420 (0.486) | 3.567 (0.463) | 3.469 (0.359) | 6.094 (0.631) |

the *T. krausbaueri* population at Spikbole, which remained in the frozen peat soil during the winter with a density maximum at a depth of 6–8 cm. A minor part of the population migrated deep enough to avoid the frost. Slightly more than 20 % of the population was found below 18 cm, which was the maximum depth of the frost. *T. krausbaueri* has been found as deep as 50 cm in a Danish soil (Haarløv, 1960), but at Spikbole the clay underlying the peat at depths varying from 15–25 cm probably acted as a barrier for further migration.

The pore diameter of the peat soil probably decreased with increasing depth (cf. Haarløv, 1955, 1960), but the soil interstices were obviously large enough for vertical migration of both adults and juveniles of the slender collembolans *T. krausbaueri* and *T. quadrispina*. Most species at Spikbole were larger than *T. krausbaueri* and were probably prevented from penetration deeper in the soil for simple mechanical reasons (cf. Weis-Fogh, 1947–48; Haarløv, 1960; Poole, 1961; Dhillon & Gibson, 1962). Abundant species such as *F. quadrioculata, F. fimetaria* coll., *I. minor* and *I. notabilis* occurred at somewhat greater depths in the "winter" than in the "summer", but the change in vertical distribution was not as pronounced as that of *T. krausbaueri.*

Another variant of vertical migration was shown by some of the surface and litter collembolans, which were found on and in the snow during mild winter days. The relative abundance and biomass of snow-living *I. viridis, E. nivalis* and *L. lignorum* amounted to about 15–25 % of their total population in the area. This is a relatively large proportion but may well be greater at certain times, and therefore the snow fauna should not be neglected when considering the total Collembola population.

The vertical distribution did not vary much during the "summer" period except for the November sampling. The distribution was somewhat more concentrated to the uppermost soil layers in August and September than in May and June. The differences, which may be assigned to the early summer drought and the unusually wet weather in July and August, were fairly small, however, when compared with the changes between "summer" and "winter".

**Abundance**

The parallel use of Macfadyen high gradient canister extractors and Tullgren funnels showed that the Tullgren funnels yielded more specimens of some of the surface-living species, which were able to escape from the sub-cores in the high gradient apparatus. Due to the larger area of the sample unit these species were also estimated with a higher precision in the Tullgren extractions. For most species, however, the Tullgren funnel extractions were less efficient compared with the high gradient canister extractions, especially for small collembolans such as *T. krausbaueri*. The combined data from the high gradient canister and Tullgren extractions gave only an insignificant addition to the total Collembola number, but since many of the surface-living species were large in size the total biomass was considerably higher when it was based on both methods than when only on the high gradient canister method.

One of the most surprising results was the difference between the abundance of total Collembola during the "summer" and "winter" periods. Most of the difference could be attributed to *T. krausbaueri* (cf. Fig. 19), but also *F. quadrioculata* had a significantly higher abundance during the "winter" than, on average, during the "summer". Several other species showed the same tendency. Valpas (1969) has demonstrated the possibility

of "laboratory hatching" of collembolans when extracting frozen soil samples. This could be a reasonable explanation for the large number of Sminthuridae, which mainly consisted of small (0.2 -0.3 mm) juveniles during the "winter". However, no abnormal hatching could have occurred for *T. krausbaueri, F. quadrioculata* or any of the other abundant species, since the size distributions were similar to those in October and November and were composed of relatively few individuals in the smallest size classes.

Common to most of the species with higher abundances during the "winter" was that they were mainly euedaphic forms. The typical soil collembolans *T. krausbaueri, F. fimetaria* coll. and *I. minor* had, for example, higher abundances during the "winter" than on any other sampling occasion. A plausible explanation is that the extraction efficiency was reduced during the "summer" samplings owing to vertical compression of the soil. When the soil was unfrozen the soil cores were vertically compressed to about 80 % of the actual sampling depth and the larger soil pores probably collapsed during the sampling, causing the collembolans to be trapped within the soil. During the "winter" the loose peat soil was frozen hard and the original soil structure was therefore maintained when the corer cut into the soil. The cores were also divided into sub-cores and put into the high gradient extractor before they had thawed. Therefore the soil collembolans could use undisturbed interstices during the "winter" extractions and probably be extracted with higher efficiency. According to this hypothesis the results of the "summer" samplings are biased and should be considered as underestimates of the real population. An important consequence of this is that the vertical distribution obtained during the "summer" period could also be biased. On average the collembolans that were not extracted probably occurred somewhat deeper than the extracted animals. The losses might thus have obscured changes in the vertical distribution during the "summer" period, and they might also have caused the differences between the vertical distributions during the "summer" and "winter" periods to be greater than in reality.

Winter peak estimates of Collembola coinciding with a remarkably low number of newly hatched individuals have also been observed by Leinaas (1976) in a spruce forest in Norway. He concluded that the extraction efficiency must have been higher during the winter than during the summer samplings. Leinaas (*op. cit.*) also concluded that the frost could result in a positive effect on the extraction efficiency by preventing compression of the soil. However, he also found increasing densities during the late autumn before the soil became frozen, and winter maxima of Collembola populations also in unfrozen coniferous forest soils. Hence, the lack of soil compression due to frost should be considered as only one of the factors improving the extraction efficiency of collembolans during the winter (Leinaas, *op. cit.*).

The fluctuations in abundance obtained during the "summer" period could sometimes be related to distinct hatching periods after which the number of individuals successively decreased in number and increased in size. This was, for example, demonstrated for the entomobryids *E. nivalis* and *L. cyaneus*. These species seemed to be univoltine at Spikbole, while they appeared to have two generations per year in a pine forest in the Netherlands (Joosse, 1969). The samplings were not frequent enough to demonstrate whether *F. quadrioculata* had two generations per year or not, but additional information from the literature supports the assumption of at least two generations. Agrell (1941) stated that *F. quadrioculata* had two generations in alpine habitats in northern Sweden, one spring generation and one summer generation. Hale (1966) assumed that *Folsomia* spp.

had two generations in an English high-altitude moorland soil, since population peaks occurred in spring and autumn. Haarlov (1960) suggested that *F. quadrioculata* could have four generations per year, at the most, in a Danish soil. Although the number of generations still may be questioned, it seems clear that *F. quadrioculata* has a distinct spring or foresummer hatching period in northwestern Europe (Agrell, 1941; Haarlov, 1960; Usher, 1970; present study).

*I. minor* had probably two generations a year at Spikbole, one spring generation and one summer generation. Agrell (1941) found only an early spring generation in northern Sweden. August density maxima of *I. minor* have been recorded by van der Drift (1951) and Usher (1970), but without separating adults and juveniles. The number of generations of *I. notabilis* could not be recorded at Spikbole, but a distinct spring hatching period occurred at least. Agrell (1941) found two generations per year in northern Sweden, of which the first was newly hatched in the early spring. Agrell (*op. cit.*), who had not studied the size distribution during the winter, assumed that adults did not hibernate. However, half of the "winter" population of *I. notabilis* at Spikbole consisted of adults. Sharma & Kevan (1963) suggested that *I. notabilis* could have at least four generations per year in a Canadian soil, where the temperature was about 6°C higher during the summer than in the soil at Spikbole. The size distribution of *T. krausbaueri* at Spikbole did not yield any information on the number of generations. According to Leinaas (1976), *T. krausbaueri* should have only one generation per year with occurrence of small juveniles in July–August. This appears to be in agreement with the findings at Spikbole where the proportion of small individuals were largest in August and September, i.e just after the hatching according to Leinaas. Other Collembola species were found in numbers that were too low to allow any analysis of hatching periods and number of generations.

The size distributions of the most abundant Collembola species showed that most of the hatching probably occurred from May to September/October, while the hatching rate must have been very low during the late autumn and the winter. Therefore, the maximum abundance of total Collembola should have been recorded at some time during the late spring, summer and early autumn, before the mortality rate had exceeded the natality rate. It is clear from the length measurements that hatching occurred during May and June as well as during the later part of the summer. The unusually high precipitation during July and August might have caused more favourable conditions during the late part of the summer, which either increased the hatching rate or reduced the mortality rate for a period of time. This might explain the relatively high abundances in August and September. Conclusions from the estimated abundances during the "summer" period must, however, be drawn with great care, since the real abundances were obscured both by imprecision (here estimated as standard error) and bias caused by inefficient extraction. An abundance peak of total Collembola during the late summer (cf. Fig. 25) is, however, in agreement with the results of Leinaas (1976) for a Norwegian coniferous forest, and Petersen (pers. comm.) for a Danish beech wood.

The most reliable estimate of the total number of Collembola is the one obtained during the "winter" with 195 000 individuals $m^{-2}$. This abundance seems to be high in comparison with most other investigations on Collembola and even the annual mean abundance of about 110 000 $m^{-2}$ is fairly high, although it appears to be a clear underestimation of the real density at Spikbole. High abundances in grassland soils have also

been reported by Haarlov (1960), who found an annual mean of 109 000 m $^{-2}$ in a Danish pasture, by Curry (1969) who estimated the annual mean to be 105 000 m $^{-2}$ in an old grassland in Ireland, and by Ghilarov & Chernov (1974) who reported a summer abundance of 99 900 m$^{-2}$ in a steppe locality in the USSR. Most studies on grassland soils have revealed lower annual mean densities, e.g. those by Baweja (1939), Glasgow (1939), Weis-Fogh (1947–48), Macfadyen (1952), Sheals (1957), Dhillon & Gibson (1962), Hale (1966), Wood (1966, 1967), Tanaka (1970b), Adams (1971), Lebrun (1971) and Ostbye *et al.* (1975), who all reported abundances within the range 8000–80 000 individuals m$^{-2}$. However, comparisons with other investigations may be misleading, since the estimates are highly dependent on the efficiency of the extraction method for a given type of soil. Many of the earlier data are based on single Tullgren funnel extraction and are probably underestimates.

Between-year fluctuations were only preliminarily studied in this investigation, but the abundances obtained in October 1969 and May 1970 during the pilot studies (cf. Appendix 1) showed no significant difference from those estimated in May and October 1971. The same species were numerically dominant in all three years, and the same species composition was recorded.

**Biomass**

The assumed underestimation in abundance during the "summer" period in 1971 also caused an underestimation of the biomass. However, the surface- and litter-dwelling collembolans contributed much more to the biomass than to the abundance, and since they were not affected by the soil compression the biomass of total Collembola was likely to be less underestimated than indicated by the abundance. The large biomass estimated during the "winter", however, probably reflected the more efficient extraction. The highest biomass values during the "summer" period were obtained at the May and November samplings. The high biomass recorded in May was partly caused by the occurrence of relatively few but large-sized *I. viridis*. The mean weights of many species, e.g. *T. krausbaueri*, *I. minor*, *I. notabilis* and *I. viridis*, increased successively from September to November and the "winter". This indicated that the biomass increased to a maximum during the late autumn, perhaps stabilized or decreased during the "winter", and possibly reached another maximum during the late spring before the overwintering adults had died and after the juveniles had begun to grow (cf. Fig. 25).

The annual mean biomass of about 140 mg dw m$^{-2}$ or about 400 mg fw m$^{-2}$ agrees with many other reports on collembolan biomasses. Annual mean biomasses around 100 mg dw m$^{-2}$ or about 300 mg fw m$^{-2}$ have been reported for a *Molinia* fen soil in England (Macfadyen, 1952) and for some high-altitude grassland soils, also in England (Hale, 1966). Higher values have been reported by Ostbye *et al.* (1975) for alpine meadows in Norway with about 200 mg dw m$^{-2}$, by Tanaka (1970b) for a Japanese grass field with about 300 mg dw m$^{-2}$, and by Lebrun (1971) for a Belgian grassland with 3160 mg fw m $^{-2}$. The latter value is probably an overestimation, since it is based on a mean live body weight of 50 μg for the actual population. In comparison the mean body weight at Spikbole was 1.3 μg dw or about 4 μg fw. The estimate of 5000 mg fw m $^{-2}$ given by Macfadyen (1963) for a grazed meadow in England seems to be too high. Lower biomasses than 100 mg dw m $^{-2}$ have been reported by Crossley *et al.* (1975), who obtained summer means of 10–16 mg dw m$^{-2}$ in ungrazed and 6–22 mg dw m$^{-2}$ in grazed grasslands in Colorado.

**Respiration**

The size dependence of the oxygen consumption rates of Collembola was estimated at $Q = 63 \cdot W^{0.73}$, when based on 29 determinations on 22 species made by several authors (Fig. 14). Dunger (1968) only used Zinkler's (1966) determinations for calculating oxygen uptake rates for different sized collembolans, but nevertheless the regression equation calculated by Dunger (*op. cit.*), $Q = 62 \cdot W^{0.74}$, differed very little from the one mentioned above, based on 22 species. In both cases $Q$ is expressed as $mm^3\ O_2\ ind^{-1}\ h^{-1}$ and $W$ as g live body weight.

Tanaka (1970b) found that the oxygen consumption rate of *Onychiurus* spp. was only about half that of *Isotoma trispinata* MacGillivray of the same weight, and questioned the use of one equation for all Collembola species. Zinkler (1966) also found that some collembolans, e.g. *Neanura muscorum* (Templeton), deviated from the general pattern and showed a much lower oxygen uptake rate than other species of the same size. However, because of the lack of more detailed data only one regression line was calculated in this study.

The regression equation used here was based on more recent studies, and the earlier measurements made by Bornebusch (1930) and Cappelletto (1939) were omitted. Determinations on alpine and arctic species, which could be suspected of having enhanced respiratory rates due to cold adaptation were also omitted. Therefore, the oxygen consumption rates of alpine and antarctic species such as *Isotoma saltans, I. hiemalis, I. klovstadi* Carpenter and *Cryptopygus antarcticus* Willem, which all have been investigated as regards the respiration rates (cf. Zinkler, 1966; Strong *et al.*, 1970; Dunkle & Strong, 1972; Tilbrook & Block, 1972; Block & Tilbrook, 1975) were not used in the calculations.

It is possible that *I. viridis, E. nivalis* and *L. lignorum*, which were found actively moving and even jumping (*I. viridis*) on the snow surface during mild winter days, were cold-adapted. However, their oxygen consumption rates were calculated in the same way as the other species at Spikbole.

The annual respiration of about 6 kcal $m^{-2}\ yr^{-1}$ of the Collembola community at Spikbole is fairly low in comparison with the relatively high abundance and biomass, but is a consequence of the low soil temperatures. Even when the assumed underestimation of the respiration during the "summer" period is considered, the annual respiration should hardly have exceeded 10–12 kcal $m^{-2}\ yr^{-1}$. The order of magnitude of the annual respiration is in agreement with many studies in temperate localities. Healey (1967b) estimated the annual respiration of total Collembola at 12 kcal $m^{-2}\ yr^{-1}$ in a *Pteridium* moorland in South Wales; Dunger (1968) recorded annual respiration values of 0.6–7.5 kcal $m^{-2}\ yr^{-1}$ in early succession stages on brown coal dumps in Germany, and Satchell (pers. comm.) reported the respiration to be 2.8 kcal $m^{-2}\ yr^{-1}$ in a deciduous woodland soil (Meathop Wood) in England. Higher values were estimated by Tanaka (1970b) for a Japanese grass field, where he calculated the annual respiration to be 36.8 kcal $m^{-2}\ yr^{-1}$ for the dominant species *Onychiurus* sp. and *Isotoma trispinata*. Lower respiration figures were recorded by Block & Tilbrook (1975) for the dominant collembolan *Cryptopygus antarctis*, which had an annual respiration of 0.4–3.7 kcal $m^{-2}\ yr^{-1}$ in a bryophyte community at Signy Island in Maritime Antarctic. Much higher respiration values (153 kcal $m^{-2}\ yr^{-1}$) have been reported by Macfadyen (1963) for the collembolans in a grazed meadow in England, but this figure is based on a mean biomass (5 g fw $m^{-2}$) that seems to be about ten times higher than normally estimated.

### Feeding habits

The feeding habits of Collembola are very variable. Most forms feed on more or less decayed plant material, fungi and bacteria, but some species are known to be carnivorous, e.g. *Friesea* species and some *Isotoma* species (Christiansen, 1964). *Friesea mirabilis* is generally considered to be a predator and may attack eggs of other collembolans (Petersen, 1971). *Isotoma viridis* has been observed to kill and devour *I. notabilis* in the laboratory even though it is normally vegetarian (Poole, 1959). Many sminthurids feed regularly on living plant material (Christiansen, *op. cit.*), and pigmented entomobryids often feed on pollen grains, algae and fungal spores (Wallwork, 1970). Despite the large number of possible feeding habits, most of the collembolans at Spikbole were classified as saprovores/microbivores. The only exception was *F. mirabilis*, which was considered to be a carnivore.

## COLEOPTERA

### Background

Coleoptera is one of the most varied arthropod groups, with a considerable number of its members in the soil fauna. Most Carabidae and Staphylinidae belong to the permanent soil fauna while, for example, Elateridae and Curculionidae often belong to the soil fauna as eggs, larvae and pupae, and emerge from the soil in the adult stage. The abundance generally seems to range from 10–5000 $m^{-2}$, while the biomass figures are usually about 0.05–5 g dw $m^{-2}$.

### Methods

The population estimates of Coleoptera were based on three different sample units, namely, the microarthropod, the macroarthropod and the lumbricid sample units. Since the macroarthropod sampler removed litter and soil cores to a depth of 3 cm, this could only be used for surface-living Coleoptera. The lumbricid soil cores were sorted by hand and only large and mobile specimens were expected to be found with any accuracy. After extraction and hand sorting the specimens were identified, counted, dried in a vacuum-drier at +60°C and weighed individually to the nearest 0.01 mg. The species determination of larvae of Carabidae, Elateridae and Curculionidae followed Larsson (1968), Palm (1972a) and Lekander (1973), respectively. Sweep-netting and collection in emergence traps enabled information to be obtained on the species composition and provided support in the identification of larvae.

The oxygen consumption rates were calculated according to different relationships between oxygen consumption rate and live body weight for different taxa within Coleoptera. The relationship for adult Carabidae and Staphylinidae was derived from data given by Bornebusch (1930), Manga (1972) and Hagvar & Ostbye (1974) (Table 20). According to the method of least squares this relationship was calculated to be $Q = 113 \cdot W^{0.739}$ at +10°Q, where $Q$ denotes $mm^3$ $O_2$ $ind^{-1}$ $h^{-1}$ and $W$ denotes g live body weight. This equation was used to calculate the oxygen uptake rates of adult

Table 20. Oxygen consumption rates of adult Carabidae and Staphylinidae. The rates are, if necessary, adjusted to +10°C by assuming $Q_{10} = 2$.

| Species | Live wt (mg) | $mm^3\ O_2\ g^{-1}\ h^{-1}$ | $mm^3\ O_2\ ind^{-1}\ h^{-1}$ | Temp. (°C) | $mm^3\ O_2\ ind^{-1}\ h^{-1}$ at+10°C | Reference |
|---|---|---|---|---|---|---|
| Carabidae | | | | | | |
| *Carabus nemoralis* | 644 | | 120.7 | 13 | 98.05 | Bornebusch (1930) |
| *Pterostichus striola* | 271 | | 40.03 | 13 | 32.51 | " |
| *P. striola* | 149 | | 38.21 | 13 | 31.04 | " |
| *Nebria brevicollis* | 84 | | 24.14 | 13 | 19.61 | " |
| *N. brevicollis* (1) | 63 | 339 | 21.36 | 10 | 21.36 | Manga (1972) |
| *N. gyllenhali* (2) | 30. | 330 | 9.900 | 10 | 9.900 | Hågvar & Østbye (1974) |
| *N. nivalis* (2) | 29 | 229 | 6.641 | 10 | 6.641 | " |
| *Patrobus septentrionis* (2) | 25 | 253 | 6.325 | 10 | 6.325 | " |
| *P. excavatus* | 15.0 | | 8.957 | 13 | 7.276 | Bornebusch (1930) |
| *Loricera pilicornis* | 22.8 | | 5.109 | 13 | 4.149 | " |
| *Calathus melanocephalus* (2) | 16 | 251 | 4.016 | 10 | 4.016 | Hågvar & Østbye (1974) |
| *Notiophilus biguttatus* | 7.5 | | 5.738 | 13 | 4.661 | Bornebusch (1930) |
| *Epaphius secalis* (female) | 2.2 | | 1.533 | 13 | 1.245 | " |
| *E. secalis* (male) | 1.2 | | 1.120 | 13 | 0.909 | " |
| Staphylinidae | | | | | | |
| *Staphylinus olens* | 247 | | 45.07 | 13 | 36.61 | " |
| Staphylinidae sp. | 1.9 | | 1.050 | 13 | 0.853 | " |

(1) Live body weight approximated from graphs showing male and female weights. Oxygen uptake rate computed as a mean of prediapause, diapause and reproductive rates.
(2) Mean live body weights approximated from graphs.

Carabidae and adult Staphylinidae as well as, due to the lack of relevant data, the rates of adult Hydrophilidae, *Choleva, Atomaria, Corticaria* and *Corticarina*. Similarly, the relationship for larvae of Staphylinidae and Hydrophilidae was calculated to be $Q = 281 \cdot W^{0.773}$ at +20°C (derived from Byzova, 1973). This equation was also used for larvae of Carabidae, Cantharidae, Lagriidae and larvae and pupae of Coleoptera sp. Prokopeva (1968) estimated the oxygen consumption rate to be 213 ± 14 $mm^3\ O_2\ g^{-1}$ fw $h^{-1}$ at 20°C for larvae of *Agriotes lineatus* L. weighing 20–37 mg fw. This rate was used to generate the equation $Q = 106 \cdot W^{0.8}$ at +20°C assuming the exponent to be 0.8 in agreement with most other exponent values. This equation was used for all Elateridae larvae at Spikbole. The oxygen consumption rates of Curculionidae larvae were calculated from the equation $Q = 89 \cdot W^{0.8}$ obtained for larvae of *Phyllobius piri* L. at 10°C (Larsson, unpubl.). In all equations the mean body weight per species and sampling occasion was used instead of the body weight ($W$) of each individual. The oxygen consumption rates of *P. piri* pupae were calculated from data given by Larsson & Lohm (1975) at different temperatures. For other Coleoptera than *P. piri* pupae the oxygen consumption rates were adjusted to the field temperature according to a $Q_{10} = 2$

between +20 and +5°C and a $Q_{10}$ = 3 below +5°C assuming an exponential relationship. Live body weight was calculated as 3 times the dry weight for adult Coleoptera and 4 times the dry weight for larval and pupal Coleoptera (cf. Edwards, 1967; Schauermann, 1973; Hågvar & Østbye, 1974).

## Results

### Species composition

The species determination of Coleoptera was mainly based on adults, while the identification of larvae could be made with acceptable accuracy only for a limited number of families. Thus, the elaterids *Agriotes lineatus* and *A. obscurus* L. could not be separated with certainty in the larval stage (cf. Nilsson, 1971) and had to be treated collectively. A total of 108 Coleoptera species were observed within the research plot (Appendix 2) and, of these, 93 species were found in the litter and soil samples. Most of the litter- and soil-dwelling Coleoptera belonged to Staphylinidae (45 species) and Carabidae (21 species), while the number of species within Curculionidae, Elateridae and other families was considerably lower.

### Vertical distribution

Most of the Coleoptera species were found in the litter and uppermost soil. However, some of the most important species with regard to the biomass were also found deeper. *Phyllobius piri* was usually found at a depth of 5–10 cm both as larva and pupa, and the *Agriotes* larvae were often found deeper than 10 cm. The vertical distribution extended to deeper layers during the "winter" when, for example, larvae of the carabid *Calathus melanocephalus* L. were not infrequently found between a depth of 10 and 30 cm. Larvae of *Trechus secalis* Payk. and *T. micros* Hbst were even found deeper than 30 cm, and larvae of *Clivina fossor* L. were sometimes found in lumbricid tunnels at a depth of 40–60 cm during the "winter". Since the vertical distribution was particularly based on the hand-sorted material, vertical migration by smaller species could not be reliably detected.

### Abundance

The abundances of the Coleoptera species are given in Tables 21–23. As no Tullgren funnel extraction was performed in May, only hand sorting and high gradient canister extraction were used for this sampling. From June onwards species that exceeded 5 cm body length were recorded by hand sorting, and the same also applied to smaller but easily detected species, such as smaller carabids and the staphylinid *Tachyporus chrysomelinus* L. Generally, estimates of smaller larvae and adults were based on Tullgren funnel extraction or, for Staphylinidae larvae, on high gradient canister extraction.

The most abundant species among the litter- and soil-inhabiting Coleoptera were the weevils *Phyllobius piri* and *P. viridicollis* Fabr. that had annual means of 480 (*s.e.* = 94) and 150 (*s.e.* = 31) individuals $m^{-2}$, respectively, in their larval and pupal stages (Table 23). *P. piri* was found as larva at the September sampling, as pupa at the October, November, "winter" and May samplings, and as above-ground adult at the June sampling. *P. viridicollis* was found as larva on all sampling occasions except the June sampling, when it was an above-ground adult. Other species with fairly high abundances were the hydrophilid *Megasternum boletophagum* Marsh. (larvae and adults) and the lagriid

Table 21. Abundance (no. $m^{-2}$) of Carabidae in 1971–72. The estimates are based on hand sorting. Standard error is given within parentheses below the corresponding mean value.
ad = adults 1 = larvae

| | | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|
| *Clivina fossor* | l | 0 | 1.1 (1.1) | 2.1 (1.5) | 2.1 (1.5) | 2.1 (1.5) | 1.5 (0.5) | 2.2 (1.3) | 1.7 (0.5) |
| *C. fossor* | ad | 4.3 (1.9) | 9.6 (6.1) | 5.3 (3.0) | 1.1 (1.1) | 3.2 (2.4) | 4.7 (1.5) | 0 | 3.1 (1.0) |
| *Dyschirius globosus* | ad | 0 | 1.1 (1.1) | 1.1 (1.1) | 0 | 0 | 0.4 (0.3) | 0 | 0.3 (0.2) |
| *Bembidion lampros* | ad | 3.2 (1.8) | 2.1 (2.1) | 3.2 (1.8) | 1.1 (1.1) | 0 | 1.9 (0.7) | 0 | 1.3 (0.5) |
| *B. guttula* | ad | 0 | 1.1 (1.1) | 2.1 (1.5) | 0 | 0 | 0.6 (0.5) | 1.1 (1.1) | 0.8 (0.5) |
| *Trechus secalis* | l | 5.3 (2.1) | 1.1 (1.1) | 1.1 (1.1) | 2.1 (2.1) | 2.1 (1.5) | 2.4 (0.8) | 5.1 (2.0) | 3.3 (0.9) |
| *T. secalis* | ad | 0 | 6.4 (4.4) | 0 | 0 | 0 | 1.3 (1.3) | 0 | 0.9 (0.9) |
| *T. micros* | ad | 0 | 1.1 (1.1) | 0 | 0 | 0 | 0.2 (0.2) | 0.5 (0.5) | 0.3 (0.3) |
| *Harpalus latus* | ad | 1.1 (1.1) | 0 | 1.1 (1.1) | 1.1 (1.1) | 1.1 (1.1) | 0.9 (0.3) | 0 | 0.7 (0.2) |
| *Bradycellus collaris* | ad | 0 | 1.1 (1.1) | 0 | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *Trichocellus placidus* | ad | 1.1 (1.1) | 3.2 (2.4) | 2.1 (1.5) | 4.3 (1.9) | 0 | 2.1 (0.8) | 1.6 (1.2) | 2.0 (0.7) |
| *Amara communis* | ad | 4.3 (2.9) | 1.1 (1.1) | 1.1 (1.1) | 0 | 0 | 1.3 (0.8) | 1.6 (0.9) | 1.4 (0.6) |
| *A. apricaria* | ad | 0 | 2.1 (1.5) | 0 | 0 | 0 | 0.4 (0.4) | 0 | 0.3 (0.3) |
| *A. consularis* | ad | 5.3 (2.6) | 2.1 (2.1) | 0 | 0 | 2.1 (2.1) | 1.9 (1.0) | 0 | 1.3 (0.7) |
| *A. aulica* | ad | 0 | 0 | 1.1 (1.1) | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *Pterostichus versicolor* | ad | 0 | 0 | 0 | 1.1 (1.1) | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *P. melanarius* | ad | 1.1 (1.1) | 0 | 0 | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *P. strenuus* | ad | 2.1 (1.5) | 2.1 (1.5) | 2.1 (1.5) | 5.3 (4.4) | 0 | 2.3 (0.9) | 3.6 (1.8) | 2.8 (0.9) |
| *P.* sp. | l | 1.1 (1.1) | 1.1 (1.1) | 1.1 (1.1) | 0 | 0 | 0.6 (0.3) | 0.5 (0.5) | 0.6 (0.3) |
| *Calathus melanocephalus* | l | 8.5 (3.8) | 4.3 (1.9) | 4.3 (1.9) | 10.7 (4.1) | 12.8 (4.2) | 8.1 (1.8) | 19.2 (5.6) | 11.8 (2.2) |
| *C. melanocephalus* | ad | 4.3 (1.9) | 3.2 (1.8) | 14.9 (6.4) | 0 | 2.1 (2.1) | 4.9 (2.6) | 0 | 3.3 (1.8) |
| *C.* cf. *micropterus* | l | 0 | 0 | 1.1 (1.1) | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *Dromius sigma* | ad | 1.1 (1.1) | 2.1 (1.5) | 3.2 (2.4) | 1.1 (1.1) | 0 | 1.5 (0.6) | 0 | 1.0 (0.4) |
| Carabidae sp. | l | 0 | 1.1 (1.1) | 0 | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| Carabidae, total | ad | 28 (4.8) | 38 (11) | 37 (8.4) | 15 (5.5) | 8.5 (4.7) | 25 (6.0) | 8.5 (4.1) | 20 (4.2) |
| Carabidae, total | l | 15 (3.7) | 8.5 (2.7) | 9.6 (3.5) | 15 (4.0) | 17 (4.6) | 13 (1.7) | 27 (6.6) | 18 (2.5) |
| Carabidae, total | l+ad | 43 (6.8) | 47 (11) | 47 (8.1) | 30 (7.2) | 26 (6.6) | 38 (4.5) | 36 (8.0) | 37 (4.0) |

Table 22. Abundance (no. $m^{-2}$) of Staphylinidae in 1971–72. Standard error is given within parentheses below the corresponding mean value

ad = adults l = larvae p = pupae

M = Macfadyen high gradient canister extraction

T = Tullgren funnel extraction

H = Hand sorting

| | | | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|---|
| *Pycnoglypta lurida* | ad | (T) | 0 | 0 | 5.3 (5.3) | 5.3 (5.3) | 10.6 (10.6) | 4.3 (2.0) | 0 | 2.8 (1.4) |
| *Olophrum assimile* | ad | (T) | 0 | 10.6 (7.1) | 5.3 (5.3) | 0 | 0 | 3.2 (2.2) | 0 | 2.1 (1.5) |
| *Stenus clavicornis* | ad | (H) | 3.2 (2.4) | 3.2 (3.2) | 3.2 (1.8) | 1.1 (1.1) | 1.1 (1.1) | 2.3 (0.6) | 0 | 1.6 (0.4) |
| *Stilicus rufipes* | ad | (H) | 1.1 (1.1) | 0 | 0 | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *Lathrobium punctatum* | ad | (H) | 0 | 0 | 0 | 1.1 (1.1) | 0 | 0.2 (0.2) | 1.3 (1.3) | 0.6 (0.5) |
| *L. geminum* | ad | (H) | 0 | 0 | 0 | 0 | 1.1 (1.1) | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *L. fulvipenne* | ad | (H) | 7.5 (5.4) | 3.2 (1.8) | 2.1 (1.5) | 1.1 (1.1) | 0 | 2.8 (1.3) | 5.8 (2.1) | 3.8 (1.2) |
| *L. longulum* | ad | (T) | 0 | 0 | 0 | 0 | 0 | 0 | 1.8 (1.8) | 0.6 (0.6) |
| *Xantholinus linearis* | ad | (H) | 2.1 (1.5) | 0 | 1.1 (1.1) | 0 | 0 | 0.6 (0.5) | 0 | 0.4 (0.3) |
| *Othius melanocephalus* | ad | (H) | 3.2 (2.4) | 1.1 (1.1) | 2.1 (1.5) | 3.2 (2.4) | 5.3 (3.8) | 3.0 (0.8) | 0.5 (0.5) | 2.2 (0.5) |
| *O. lapidicola* | ad | (H) | 0 | 2.1 (1.5) | 5.3 (3.4) | 1.1 (1.1) | 0 | 1.7 (1.0) | 0 | 1.1 (0.7 |
| *Philonthus varius* | ad | (H) | 0 | 0 | 1.1 (1.1) | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *Staphylinus fuscatus* | ad | (H) | 1.1 (1.1) | 0 | 0 | 0 | 0 | 0.2 (0.2) | 0.5 (0.5) | 0.3 (0.3) |
| *Quedius fuliginosus* | ad | (H) | 0 | 0 | 1.1 (1.1) | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *Q. curtipennis* | ad | (H) | 0 | 0 | 6.4 (4.4) | 4.3 (2.5) | 2.1 (2.1) | 2.6 (1.3) | 0.5 (0.5) | 1.9 (0.9) |
| *Q. picipennis* | ad | (H) | 0 | 0 | 1.1 (1.1) | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *Q. fulvicollis* | ad | (H) | 4.3 (1.9) | 3.2 (1.8) | 9.6 (4.9) | 5.3 (3.0) | 2.1 (1.5) | 4.9 (1.3) | 3.6 (1.9) | 4.5 (1.1) |
| *Mycetoporus splendidus* | ad | (T) | 0 | 0 | 0 | 5.3 (5.3) | 0 | 1.1 (1.1) | 0 | 0.7 (0.7) |
| *Conosoma pedicularium* | ad | (T) | 0 | 0 | 0 | 5.3 (5.3) | 5.3 (5.3) | 2.1 (1.3) | 10.3 (5.8) | 4.9 (2.2) |
| *Tachyporus chrysomelinus* | ad | (H) | 7.5 (2.7) | 5.3 (2.6) | 9.6 (3.8) | 4.3 (2.5) | 4.3 (3.3) | 6.2 (1.1) | 2.7 (1.3) | 5.0 (0.9) |
| *T. pulchellus* | ad | (T+H) | 1.1 (1.1) | 0 | 0 | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *Tachinus rufipes* | ad | (H) | 4.3 (2.5) | 2.1 (1.5) | 0 | 1.1 (1.1) | 0 | 1.5 (0.8) | 0 | 1.0 (0.6) |
| *T. rufipennis* | ad | (H) | 0 | 0 | 1.1 (1.1) | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *T. corticinus* | ad | (T+H) | 1.1 (1.1) | 0 | 0 | 0 | 10.6 (7.1) | 2.3 (2.1) | 4.3 (4.3) | 3.0 (2.0) |
| *Myllaena minuta* | ad | (T) | 0 | 0 | 0 | 0 | 0 | 0 | 1.8 (1.8) | 0.6 (0.6) |
| *Schistoglossa gemina* | ad | (T) | 0 | 0 | 16.0 (8.2) | 0 | 0 | 3.2 (3.2) | 0 | 2.1 (2.1) |
| *Amischa analis* | ad | (T) | 0 | 5.3 (5.3) | 16.0 (8.2) | 10.6 (7.1) | 5.3 (5.3) | 7.5 (2.8) | 9.7 (5.2) | 8.2 (2.5) |
| *A. cavifrons* | ad | (T) | 0 | 16.0 (8.2) | 53.2 (21.0) | 42.6 (17.4) | 26.6 (11.9) | 27.7 (9.5) | 76.6 (18.4) | 44.0 (8.8) |
| *Sipalia circellaris* | ad | (T) | 0 | 0 | 5.3 (5.3) | 10.6 (10.6) | 10.6 (10.6) | 5.3 (2.4) | 7.9 (4.9) | 6.2 (2.3) |
| *Atheta britteni* | ad | (T) | 0 | 0 | 0 | 5.3 (5.3) | 0 | 1.1 (1.1) | 36.2 (11.3) | 12.8 (3.9) |
| *A. fungi* | ad | (T+H) | 7.5 (4.4) | 10.6 (7.1) | 21.3 (11.8) | 53.2 (15.9) | 63.8 (24.9) | 31.3 (11.5) | 51.4 (21.0) | 38.0 (10.4) |
| *Oxypoda advena* | ad | (T) | 0 | 0 | 10.6 (7.1) | 0 | 5.3 (5.3) | 3.2 (2.2) | 0 | 2.1 (1.5) |
| *O. soror* | ad | (T) | 0 | 0 | 5.3 (5.3) | 0 | 0 | 1.1 (1.1) | 0 | 0.7 (0.7) |
| *Aleochara brevipennis* | ad | (T) | 0 | 5.3 (5.3) | 0 | 0 | 0 | 1.1 (1.1) | 8.5 (5.5) | 3.5 (2.0) |
| Staphylinidae, total | ad | (T+H) | 44 | 68 | 182 | 161 | 154 | 122 (28) | 223 (45) | 156 (24) |
| Staphylinidae | l | (M) | 185 (99) | 432 (178) | 432 (178) | 494 (124) | 432 (153) | 395 (54) | 112 (21) | 301 (37) |
| Staphylinidae | p | (H) | 0 | 4.3 (2.5) | 1.1 (1.1) | 0 | 0 | 1.1 (0.9) | 0 | 0.7 (0.6) |
| Staphylinidae, total | l+p+ad | (M+T+H) | 229 | 505 | 615 | 655 | 586 | 518 (77) | 335 (58) | 457 (55) |

Table 23. Abundance (no. $m^{-2}$) of soil- or surface-dwelling Coleoptera not belonging to Carabidae or Staphylinidae and the total abundance of Coleoptera in 1971–72. Standard error is given within parentheses below the corresponding mean value.
ad = adults l = larvae p = pupae
M = Macfadyen high gradient canister extraction
T = Tullgren funnel extraction
H = Hand sorting

| | | | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|---|
| *Megasternum boletophagum* | l | (M+T) | 0 | 5.3 (5.3) | 351.1 (97.5) | 175.5 (65.5) | 74.5 (18.1) | 121.3 (65.7) | 131.8 (24.6) | 124.8 (44.5) |
| *M. boletophagum* | ad | (M+T) | 0 | 0 | 21.3 (11.8) | 26.6 (14.3) | 16.0 (8.2) | 12.8 (5.5) | 15.1 (6.0) | 13.5 (4.2) |
| *Choleva angustata* | ad | (H) | 0 | 0 | 0 | 0 | 1.1 (1.1) | 0.2 (0.2) | 0 | 0.1 (0.1) |
| Cantharidae sp. | l | (T+H) | 7.5 (4.4) | 31.9 (11.8) | 10.6 (7.1) | 10.6 (7.1) | 5.3 (5.3) | 13.2 (4.8) | 1.8 (1.8) | 9.4 (3.3) |
| *Corymbites aeneus* | l | (H) | 0 | 0 | 1.1 (1.1) | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *Agriotes lineatus/obscurus* | l | (H) | 32.0 (11.6) | 40.5 (12.6) | 6.4 (2.6) | 17.1 (6.4) | 7.5 (3.5) | 20.7 (6.8) | 15.5 (4.4) | 19.0 (4.8) |
| *Atomaria analis* | ad | (T+H) | 0 | 0 | 0 | 10.6 (7.1) | 0 | 2.1 (2.1) | 0 | 1.4 (1.4) |
| *A. atricapilla* | ad | (T+H) | 2.1 (2.1) | 5.3 (5.3) | 0 | 37.2 (22.5) | 16.0 (8.2) | 12.1 (6.9) | 27.0 (12.7) | 17.1 (6.3) |
| *Corticaria impressa* | ad | (T+H) | 0 | 0 | 0 | 5.3 (5.3) | 0 | 1.1 (1.1) | 0 | 0.7 (0.7) |
| *Corticarina fuscula* | ad | (T+H) | 0 | 0 | 0 | 0 | 0 | 0 | 1.8 (1.8) | 0.6 (0.6) |
| *Lagria hirta* | l | (T+H) | 1.1 (1.1) | 5.3 (5.3) | 234.0 (87.0) | 234.0 (169.8) | 16.0 (8.2) | 98.1 (55.6) | 29.0 (15.8) | 75.0 (37.4) |
| *Phyllobius piri* | l+p | (H) | 544.0 (92.0) | 0 | 806.4 (133.6) | 538.6 (68.2) | 456.0 (116.4) | 469.0 (131.3) | 512.1 (97.8) | 483.4 (93.4) |
| *P. viridicollis* | l+p | (H) | 68.3 (22.2) | 0 | 84.3 (20.6) | 155.7 (25.5) | 252.8 (60.1) | 112.2 (43.0) | 217.8 (34.5) | 147.4 (30.9) |
| Curculionidae sp. | l | (H) | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 (0.5) | 0.2 (0.2) |
| Coleoptera sp. | l | (M+T) | 0 | 111.7 (36.8) | 5.3 (5.3) | 0 | 0 | 23.4 (22.1) | 1.8 (1.8) | 16.2 (14.8) |
| Coleoptera sp. | p | (H) | 0 | 0 | 0 | 1.1 (1.1) | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| Total of species above | l+p+ad | (T+H) | 655 | 200 | 1521 | 1212 | 845 | 887 | 954 | 909 |
| Coleoptera, total | l+p+ad | (M+T+H) | 927 | 752 | 2183 | 1897 | 1457 | 1443 (274) | 1325 (146) | 1404 (189) |

*Lagria hirta* L. (larvae) with annual means of about 140 and 75 individuals $m^{-2}$ (Table 23). Some of the Staphylinidae species were also relatively abundant, for example *Amischa cavifrons* Sharp and *Atheta fungi* Grav. that both had annual mean numbers of about 40 individuals $m^{-2}$ in the adult stage (Table 22). These are certainly underestimations of the total abundance of the species, since the larval abundance was not included owing to identification problems. Curculionidae with about 630 individuals $m^{-2}$ and Staphylinidae with about 460 individuals $m^{-2}$ on an annual basis constituted the numerically dominant groups within Coleoptera, while the numerical importance of Hydrophilidae (140 $m^{-2}$) and Lagriidae (75 $m^{-2}$) was considerably lower (Tables 21–23).

The population fluctuations were very distinct for certain species; an example being *P. piri* with a population low in June after the adults had emerged from the soil, and a population peak during the mid-summer period after egg-hatching (cf. Fig. 24 and also Axelsson *et al.*, 1973a). Other species with pronounced peak abundances were *Megaster-*

*num boletophagum* and *Lagria hirta*, both having a large number of young larvae in September. Peak numbers of very small larvae of Cantharidae and of unidentified Coleoptera in June indicated that these species must have hatched in the early summer.

**Biomass**

The biomass of Coleoptera was dominated by *P. piri* on all sampling occasions except for the June sampling when the *Agriotes* larvae had the highest biomass (Tables 24–26). The annual mean biomass of about 2200 mg dw $m^{-2}$ of *P. piri* accounted for nearly 80 % of the annual mean of total Coleoptera of 2900 (*s.e.* = 420) mg dw $m^{-2}$. Other species that contributed significantly to the total annual mean biomass were *Agriotes lineatus/obscurus* (larvae) with 230 (*s.e.* = 44) mg dw $m^{-2}$, *Phyllobius viridicollis* (larvae and pupae) with 81 (*s.e.* = 19) mg dw $m^{-2}$ and *Calathus melanocephalus* (larvae and adults) with 37 (*s.e.* = 12) mg dw $m^{-2}$. The families that dominated the biomass were Curculionidae, Elateridae, Carabidae and Staphylinidae with annual means of about 2300, 230, 130 and 130 mg dw $m^{-2}$, respectively. The contribution by other families, for example Hydrophilidae (about 20 mg $m^{-2}$) and Cantharidae (about 10 mg $m^{-2}$) were much smaller.

The biomass of total Coleoptera fluctuated considerably over the year with a maximum in September (about 4100 mg dw $m^{-2}$) and a minimum in June (about 600 mg dw $m^{-2}$) (Table 26). These fluctuations chiefly reflected the variations in the biomass of *P. piri* (cf. Fig. 24). The biomass of Coleoptera less *P. piri* showed insignificant fluctuations around a mean value of about 620 mg dw $m^{-2}$ (cf. Fig. 24). The fluctuations were small mainly because the biomasses of Carabidae, Staphylinidae and the *Agriotes* species balanced each other to a great extent.

**Respiration**

The oxygen consumption rates and the annual respiration of Coleoptera are presented in Tables 27–29. The annual respiration was dominated by *P. piri*, which accounted for 24 (*s.e.* = 12) kcal $m^{-2}$ $yr^{-1}$ or 56 % of the total annual respiration of 43 (*s.e.* = 13) kcal $m^{-2}$ $yr^{-1}$. Other species with a high respiration were *Agriotes lineatus/obscurus* with about 2.8 kcal $m^{-2}$ $yr^{-1}$, *P. viridicollis* with 2.1 kcal $m^{-2}$ $yr^{-1}$, *Calathus melanocephalus* with 1.4 kcal $m^{-2}$ $yr^{-1}$ and *Megasternum boletophagum* with 1.3 kcal $m^{-2}$ $yr^{-1}$. The families contributing most to the annual respiration were Curculionidae, Staphylinidae, Carabidae and Elateridae with 26, 6.5, 4.5 and 2.9 kcal $m^{-2}$ $yr^{-1}$, respectively.

The oxygen consumption rates of *P. piri* fluctuated markedly over the year. The peak oxygen uptake rate was estimated in September, when practically all larvae had reached instar V (cf. Axelsson *et al.*, 1973a). Much lower oxygen uptake rates were calculated in October, November and during the "winter" when the population consisted of pupae, and when the soil temperature was lower. The difference between the May estimate, when the temperature was higher but the population level lower than in September, and the September estimate, particularly reflects the difference between pupal and larval oxygen consumption (cf. Table 55). The oxygen consumption rates of Coleoptera less *P. piri* showed relatively small fluctuations over the year, with about 10–15 $cm^3$ $O_2$ $m^{-2}$ $day^{-1}$ during the "summer" samplings and about 6 $cm^3$ $O_2$ $m^{-2}$ $day^{-1}$ during the "winter".

Table 24. Biomass (mg dry weight $m^{-2}$) of Carabidae in 1971–72. The estimates are based on hand sorting. Standard error is given within parentheses below the corresponding mean value. + denotes a value less than 0.05.
ad = adults l = larvae

| | | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|
| *Clivina fossor* | l | 0 | 0.5 (0.5) | 1.4 (1.3) | 0.5 (0.3) | 3.7 (2.5) | 1.2 (0.7) | 2.5 (1.8) | 1.7 (0.8) |
| *C. fossor* | ad | 8.8 (4.0) | 22.7 (14.4) | 14.4 (8.1) | 1.7 (1.7) | 5.4 (4.3) | 10.6 (3.7) | 0 | 7.1 (2.5) |
| *Dyschirius globosus* | ad | 0 | 0.4 (0.4) | 0.3 (0.3) | 0 | 0 | 0.1 (0.1) | 0 | 0.1 (0.1) |
| *Bembidion lampros* | ad | 1.5 (0.8) | 0.8 (0.8) | 1.9 (1.0) | 0.6 (0.6) | 0 | 0.9 (0.4) | 0 | 0.6 (0.3) |
| *B. guttula* | ad | 0 | 0.4 (0.4) | 1.5 (1.1) | 0 | 0 | 0.4 (0.3) | 0.7 (0.7) | 0.5 (0.3) |
| *Trechus secalis* | l | 2.7 (1.1) | 0.5 (0.5) | 0.1 (0.1) | 0.3 (0.3) | 0.6 (0.4) | 0.8 (0.5) | 1.4 (0.6) | 1.0 (0.4) |
| *T. secalis* | ad | 0 | 2.2 (1.6) | 0 | 0 | 0 | 0.4 (0.4) | 0 | 0.3 (0.3) |
| *T. micros* | ad | 0 | 0.7 (0.7) | 0 | 0 | 0 | 0.2 (0.2) | 0.4 (0.4) | 0.2 (0.2) |
| *Harpalus latus* | ad | 17.8 (17.8) | 0 | 23.3 (23.3) | 16.2 (16.2) | 16.8 (16.8) | 14.9 (3.9) | 0 | 9.9 (2.6) |
| *Bradycellus collaris* | ad | 0 | 1.3 (1.3) | 0 | 0 | 0 | 0.3 (0.3) | 0 | 0.2 (0.2) |
| *Trichocellus placidus* | ad | 1.7 (1.7) | 4.7 (3.5) | 2.1 (1.7) | 6.9 (3.1) | 0 | 3.1 (1.3) | 2.4 (1.7) | 2.9 (1.0) |
| *Amara communis* | ad | 25.6 (17.5) | 7.0 (7.0) | 14.2 (14.2) | 0 | 0 | 9.4 (4.9) | 10.2 (5.4) | 9.7 (3.7) |
| *A. apricaria* | ad | 0 | 16.9 (12.0) | 0 | 0 | 0 | 3.4 (3.4) | 0 | 2.3 (2.3) |
| *A. consularis* | ad | 67.3 (37.1) | 29.0 (29.0) | 0 | 0 | 33.4 (33.4) | 26.0 (12.5) | 0 | 17.3 (8.4) |
| *A. aulica* | ad | 0 | 0 | 44.2 (44.2) | 0 | 0 | 8.8 (8.8) | 0 | 5.9 (5.9) |
| *Pterostichus versicolor* | ad | 0 | 0 | 0 | 10.8 (10.8) | 0 | 2.2 (2.2) | 0 | 1.4 (1.4) |
| *P. melanarius* | ad | 49.0 (49.0) | 0 | 0 | 0 | 0 | 9.8 (9.8) | 0 | 6.5 (6.5) |
| *P. strenuus* | ad | 7.4 (5.1) | 8.7 (6.0) | 11.2 (7.8) | 21.5 (18.2) | 0 | 9.8 (3.5) | 10.9 (5.4) | 10.1 (2.9) |
| *P.* sp. | l | 44.5 (44.5) | 23.7 (23.7) | 4.4 (4.4) | 0 | 0 | 14.5 (8.7) | 21.7 (21.7) | 16.9 (9.3) |
| *Calathus melanocephalus* | l | 20.0 (8.1) | 6.7 (3.2) | 3.9 (1.8) | 14.5 (7.0) | 15.0 (4.8) | 12.0 (3.0) | 27.9 (6.1) | 17.3 (2.9) |
| *C. melanocephalus* | ad | 17.9 (8.2) | 15.0 (8.0) | 104.6 (43.6) | 0 | 11.6 (11.6) | 29.8 (19.0) | 0 | 19.9 (12.7) |
| *C.* cf. *micropterus* | l | 0 | 0 | 2.8 (2.8) | 0 | 0 | 0.6 (0.6) | 0 | 0.4 (0.4) |
| *Dromius sigma* | ad | 0.4 (0.4) | 1.0 (0.7) | 1.9 (1.4) | 0.5 (0.5) | 0 | 0.8 (0.4) | 0 | 0.5 (0.3) |
| Carabidae sp. | l | 0 | 0.2 (0.2) | 0 | 0 | 0 | + | 0 | + |
| Carabidae, total | l | 67 (44) | 32 (24) | 13 (6.4) | 15 (6.9) | 19 (4.6) | 29 (10) | 53 (24) | 37 (11) |
| Carabidae, total | ad | 197 (70) | 111 (44) | 220 (80) | 58 (25) | 67 (41) | 131 (34) | 25 (9.5) | 95 (23) |
| Carabidae, total | l+ad | 265 (86) | 143 (50) | 232 (80) | 73 (26) | 87 (42) | 160 (39) | 78 (25) | 133 (28) |

Table 25. Biomass (mg dry weight $m^{-2}$) of Staphylinidae in 1971–72. Standard error is given within parentheses below the corresponding mean value. + denotes a value less than 0.05.
ad = adults · l = larvae p = pupae

| | | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|
| *Pycnoglypta lurida* | ad | 0 | 0 | 1.9 (1.9) | 1.9 (1.9) | 3.8 (3.8) | 1.5 (0.8) | 0 | 1.0 (0.5) |
| *Olophrum assimile* | ad | 0 | 9.6 (6.4) | 4.8 (4.8) | 0 | 0 | 2.9 (2.0) | 0 | 1.9 (1.3) |
| *Stenus clavicornis* | ad | 3.3 (2.4) | 3.8 (3.8) | 2.9 (1.9) | 2.1 (2.1) | 1.4 (1.4) | 2.7 (0.5) | 0 | 1.8 (0.3) |
| *Stilicus rufipes* | ad | 1.2 (1.2) | 0 | 0 | 0 | 0 | 0.2 (0.2) | 0 | 0.2 (0.2) |
| *Lathrobium punctatum* | ad | 0 | 0 | 0 | 1.5 (1.5) | 0 | 0.3 (0.3) | 3.1 (3.1) | 1.2 (1.1) |
| *L. geminum* | ad | 0 | 0 | 0 | 0 | 2.4 (2.4) | 0.5 (0.5) | 0 | 0.3 (0.3) |
| *L. fulvipenne* | ad | 14.4 (10.4) | 8.5 (5.1) | 5.4 (4.1) | 3.0 (3.0) | 0 | 6.3 (2.5) | 11.2 (4.0) | 7.9 (2.1) |
| *L. longulum* | ad | 0 | 0 | 0 | 0 | 0 | 0 | 0.6 (0.6) | 0.2 (0.2) |
| *Xantholinus linearis* | ad | 1.9 (1.3) | 0 | 1.1 (1.1) | 0 | 0 | 0.6 (0.4) | 0 | 0.4 (0.3) |
| *Othius melanocephalus* | ad | 2.7 (2.0) | 0.6 (0.6) | 2.4 (1.7) | 3.7 (2.8) | 4.8 (3.4) | 2.8 (0.8) | 0.5 (0.5) | 2.1 (0.5) |
| *O. lapidicola* | ad | 0 | 1.9 (1.4) | 6.5 (4.1) | 1.0 (1.0) | 0 | 1.9 (1.2) | 0 | 1.3 (0.8) |
| *Philonthus varius* | ad | 0 | 0 | 1.9 (1.9) | 0 | 0 | 0.4 (0.4) | 0 | 0.3 (0.3) |
| *Staphylinus fuscatus* | ad | 11.2 (11.2) | 0 | 0 | 0 | 0 | 2.3 (2.3) | 4.1 (4.1) | 2.9 (2.1) |
| *Quedius fuliginosus* | ad | 0 | 0 | 9.6 (9.6) | 0 | 0 | 1.9 (1.9) | 0 | 1.3 (1.3) |
| *Q. curtipennis* | ad | 0 | 0 | 42.4 (28.2) | 44.8 (25.8) | 17.6 (17.6) | 21.0 (9.8) | 5.9 (5.9) | 15.9 (6.9) |
| *Q. picipennis* | ad | 0 | 0 | 12.8 (12.8) | 0 | 0 | 2.6 (2.6) | 0 | 1.7 (1.7) |
| *Q. fulvicollis* | ad | 4.5 (2.0) | 4.2 (2.3) | 15.6 (8.4) | 8.6 (2.3) | 4.7 (3.4) | 7.5 (2.2) | 4.1 (2.1) | 6.4 (1.7) |
| *Mycetoporus splendidus* | ad | 0 | 0 | 0 | 2.1 (2.1) | 0 | 0.4 (0.4) | 0 | 0.3 (0.3) |
| *Conosoma pedicularium* | ad | 0 | 0 | 0 | 1.3 (1.3) | 1.3 (1.3) | 0.5 (0.4) | 2.6 (1.5) | 1.2 (0.6) |
| *Tachyporus chrysomelinus* | ad | 3.4 (1.2) | 2.7 (1.3) | 6.4 (2.7) | 2.9 (2.0) | 3.0 (2.4) | 3.7 (0.7) | 1.5 (0.8) | 3.0 (0.6) |
| *T. pulchellus* | ad | 0.3 (0.3) | 0 | 0 | 0 | 0 | 0.1 (0.1) | 0 | + |
| *Tachinus rufipes* | ad | 8.0 (4.8) | 4.3 (3.2) | 0 | 1.0 (1.0) | 0 | 2.7 (1.6) | 0 | 1.8 (1.1) |
| *T. rufipennis* | ad | 0 | 0 | 4.5 (4.5) | 0 | 0 | 0.9 (0.9) | 0 | 0.6 (0.6) |
| *T. corticinus* | ad | 0.5 (0.5) | 0 | 0 | 0 | 7.5 (5.0) | 1.6 (1.5) | 3.0 (3.0) | 2.1 (1.4) |
| *Myllaena minuta* | ad | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 (0.1) | + |
| *Schistoglossa gemina* | ad | 0 | 0 | 1.3 (0.7) | 0 | 0 | 0.3 (0.3) | 0 | 0.2 (0.2) |
| *Amischa analis* | ad | 0 | 0.6 (0.6) | 1.9 (1.0) | 1.3 (0.9) | 0.6 (0.6) | 0.9 (0.4) | 1.2 (0.7) | 1.0 (0.3) |
| *A. cavifrons* | ad | 0 | 1.9 (1.0) | 6.4 (2.6) | 5.1 (2.1) | 3.2 (1.5) | 3.3 (1.2) | 9.2 (2.2) | 5.3 (1.1) |
| *Sipalia circellaris* | ad | 0 | 0 | 0.8 (0.8) | 1.6 (1.6) | 1.6 (1.6) | 0.8 (0.4) | 1.2 (0.8) | 0.9 (0.4) |
| *Atheta britteni* | ad | 0 | 0 | 0 | 0.5 (0.5) | 0 | 0.1 (0.1) | 3.6 (1.2) | 1.3 (0.4) |
| *A. fungi* | ad | 1.7 (1.1) | 1.7 (1.2) | 3.4 (1.9) | 8.5 (2.6) | 10.2 (4.0) | 5.1 (1.8) | 8.2 (3.4) | 6.1 (1.7) |
| *Oxypoda advena* | ad | 0 | 0 | 1.9 (1.3) | 0 | 1.0 (1.0) | 0.6 (0.4) | 0 | 0.4 (0.3) |
| *O. soror* | ad | 0 | 0 | 0.7 (0.7) | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *Aleochara brevipennis* | ad | 0 | 6.4 (6.4) | 0 | 0 | 0 | 1.3 (1.3) | 10.2 (6.6) | 4.3 (2.4) |
| Staphylinidae, total | ad | 53 | 46 | 135 | 91 | 63 | 78 (17) | 70 (14) | 75 (12) |
| Staphylinidae | l | 1.2 (0.9) | 7.4 (4.9) | 22 (12) | 65 (30) | 171 (81) | 53 (32) | 51 (13) | 52 (22) |
| Staphylinidae | p | 0 | 11 (6.8) | 0.8 (0.8) | 0 | 0 | 2.3 (2.1) | 0 | 1.5 (1.4) |
| Staphylinidae, total | l+p+ad | 54 | 64 | 157 | 157 | 234 | 133 (34) | 121 (20) | 129 (24) |

Table 26. Biomass (mg dry weight $m^{-2}$) of soil- or surface-dwelling Coleoptera not belonging to Carabidae or Staphylinidae and the total biomass of Coleoptera in 1971–72. Standard error is given within parentheses below the corresponding mean value.
ad = adults l = larvae p = pupae

| | | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|
| *Megasternum boletophagum* | l | 0 | 0.3 (0.3) | 17.7 (6.2) | 16.9 (7.6) | 10.5 (3.0) | 9.1 (3.9) | 19.2 (2.9) | 12.4 (2.8) |
| *M. boletophagum* | ad | 0 | 0 | 11.7 (6.5) | 14.6 (7.9) | 8.8 (4.5) | 7.0 (3.0) | 8.3 (3.4) | 7.4 (2.3) |
| *Choleva angustata* | ad | 0 | 0 | 0 | 0 | 1.6 (1.6) | 0.3 (0.3) | 0 | 0.2 (0.2) |
| Cantharidae sp. | l | 40.9 (27.2) | 0.1 (0.1) | 2.6 (2.2) | 13.0 (8.8) | 7.2 (7.2) | 12.8 (7.4) | 5.8 (5.8) | 10.4 (5.3) |
| *Corymbites aeneus* | l | 0 | 0 | 4.9 (4.9) | 0 | 0 | 1.0 (1.0) | 0 | 0.7 (0.7) |
| *Agriotes lineatus/obscurus* | l | 352.6 (101.0) | 405.5 (110.0) | 156.4 (67.5) | 251.9 (99.6) | 96.9 (52.7) | 252.6 (57.9) | 190.9 (58.9) | 232.1 (43.3) |
| *Atomaria analis* | ad | 0 | 0 | 0 | 2.1 (1.5) | 0 | 0.4 (0.4) | 0 | 0.3 (0.3) |
| *A. atricapilla* | ad | 0.6 (0.6) | 1.6 (1.6) | 0 | 11.2 (6.8) | 4.8 (2.5) | 3.6 (2.1) | 8.1 (3.8) | 5.1 (1.9) |
| *Corticaria impressa* | ad | 0 | 0 | 0 | 1.1 (1.1) | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *Corticarina fuscula* | ad | 0 | 0 | 0 | 0 | 0 | 0 | 0.4 (0.4) | 0.1 (0.1) |
| *Lagria hirta* | l | 0.9 (0.9) | 0.1 (0.1) | 20.6 (8.2) | 29.7 (20.9) | 2.0 (1.2) | 10.7 (6.1) | 5.5 (2.9) | 8.9 (4.2) |
| *Phyllobius piri* | l+p | 2040.0 (344.9) | 0 | 3465.8 (576.2) | 2867.5 (361.8) | 2416.8 (614.8) | 2158.0 (589.6) | 2386.2 (455.7) | 2234.1 (421.4) |
| *P. viridicollis* | l+p | 81.9 (26.6) | 0 | 20.2 (5.1) | 54.6 (9.1) | 151.8 (36.0) | 61.7 (26.6) | 119.8 (19.0) | 81.1 (18.8) |
| Curculionidae sp. | l | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 (0.5) | 0.2 (0.2) |
| Coleoptera sp. | l | 0 | 1.0 (0.6) | 1.3 (1.3) | 0 | 0 | 0.5 (0.3) | 0.2 (0.2) | 0.4 (0.2) |
| Coleoptera sp. | p | 0 | 0 | 0 | 5.3 (5.3) | 0 | 1.1 (1.1) | 0 | 0.7 (0.7) |
| Total of species above | l+p+ad | 2517 | 409 | 3701 | 3268 | 2700 | 2519 | 2745 | 2594 |
| Coleoptera, total | l+p+ad | 2836 | 616 | 4090 | 3498 | 3021 | 2812 (591) | 2944 (427) | 2856 (419) |

Table 27. Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) and annual respiration (kcal $m^{-2}$) of Carabidae in 1971–72. Standard error is given within parentheses below the corresponding mean value. + denotes a value less than 0.005.
ad = adults l = larvae

| | | Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) | | | | | | | | Annual respiration (kcal $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|---|
| | | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual | |
| *Clivina fossor* | l | 0 | 0.03 (0.03) | 0.06 (0.06) | 0.02 (0.02) | 0.07 (0.05) | 0.04 (0.02) | 0.04 (0.03) | 0.04 (0.02) | 0.07 (0.03) |
| *C. fossor* | ad | 0.27 (0.13) | 0.70 (0.44) | 0.37 (0.21) | 0.04 (0.04) | 0.08 (0.06) | 0.29 (0.12) | 0 | 0.19 (0.08) | 0.34 (0.14) |
| *Dyschirius globosus* | ad | 0 | 0.02 (0.02) | 0.01 (0.01) | 0 | 0 | 0.01 (0.01) | 0 | + | 0.01 (0.01) |
| *Bembidion lampros* | ad | 0.07 (0.04) | 0.04 (0.04) | 0.07 (0.04) | 0.02 (0.02) | 0 | 0.04 (0.02) | 0 | 0.03 (0.01) | 0.05 (0.02) |
| *B. guttula* | ad | 0 | 0.02 (0.02) | 0.05 (0.04) | 0 | 0 | 0.01 (0.01) | 0.01 (0.01) | 0.01 (0.01) | 0.02 (0.02) |
| *Trechus secalis* | l | 0.15 (0.06) | 0.03 (0.03) | + | 0.01 (0.01) | 0.02 (0.02) | 0.04 (0.03) | 0.03 (0.02) | 0.04 (0.02) | 0.07 (0.04) |
| *T. secalis* | ad | 0 | 0.11 (0.08) | 0 | 0 | 0 | 0.02 (0.02) | 0 | 0.01 (0.01) | 0.03 (0.03) |
| *T. micros* | ad | 0 | 0.03 (0.03) | 0 | 0 | 0 | 0.01 (0.01) | 0.01 (0.01) | 0.01 (0.01) | 0.01 (0.01) |
| *Harpalus latus* | ad | 0.33 (0.33) | 0 | 0.37 (0.37) | 0.21 (0.21) | 0.15 (0.15) | 0.21 (0.07) | 0 | 0.14 (0.05) | 0.25 (0.08) |
| *Bradycellus collaris* | ad | 0 | 0.05 (0.05) | 0 | 0 | 0 | 0.01 (0.01) | 0 | 0.01 (0.01) | 0.01 (0.01) |
| *Trichocellus placidus* | ad | 0.06 (0.06) | 0.16 (0.12) | 0.06 (0.05) | 0.16 (0.08) | 0 | 0.09 (0.04) | 0.03 (0.02) | 0.07 (0.03) | 0.12 (0.04) |
| *Amara communis* | ad | 0.59 (0.40) | 0.16 (0.16) | 0.27 (0.27) | 0 | 0 | 0.20 (0.11) | 0.08 (0.05) | 0.16 (0.08) | 0.29 (0.13) |
| *A. apricaria* | ad | 0 | 0.37 (0.27) | 0 | 0 | 0 | 0.07 (0.07) | 0 | 0.05 (0.05) | 0.09 (0.09) |
| *A. consularis* | ad | 1.30 (0.71) | 0.56 (0.56) | 0 | 0 | 0.30 (0.30) | 0.43 (0.24) | 0 | 0.29 (0.16) | 0.50 (0.29) |
| *A. aulica* | ad | 0 | 0 | 0.53 (0.53) | 0 | 0 | 0.11 (0.11) | 0 | 0.07 (0.07) | 0.12 (0.12) |
| *Pterostichus versicolor* | ad | 0 | 0 | 0 | 0.15 (0.15) | 0 | 0.03 (0.03) | 0 | 0.02 (0.02) | 0.04 (0.04) |
| *P. melanarius* | ad | 0.68 (0.68) | 0 | 0 | 0 | 0 | 0.14 (0.14) | 0 | 0.09 (0.09) | 0.16 (0.16) |
| *P. strenuus* | ad | 0.20 (0.14) | 0.24 (0.17) | 0.25 (0.18) | 0.40 (0.35) | 0 | 0.22 (0.07) | 0.11 (0.06) | 0.18 (0.05) | 0.32 (0.09) |
| *P.* sp. | l | 0.92 (0.92) | 0.57 (0.57) | 0.13 (0.13) | 0 | 0 | 0.32 (0.19) | 0.16 (0.16) | 0.27 (0.14) | 0.47 (0.24) |
| *Calathus melanocephalus* | l | 0.80 (0.33) | 0.29 (0.14) | 0.16 (0.08) | 0.45 (0.22) | 0.33 (0.11) | 0.41 (0.11) | 0.45 (0.10) | 0.42 (0.08) | 0.74 (0.14) |
| *C. melanocephalus* | ad | 0.43 (0.20) | 0.36 (0.19) | 2.07 (0.87) | 0 | 0.13 (0.13) | 0.60 (0.38) | 0 | 0.40 (0.26) | 0.70 (0.45) |
| *C.* cf. *micropterus* | l | 0 | 0 | 0.09 (0.09) | 0 | 0 | 0.02 (0.02) | 0 | 0.01 (0.01) | 0.02 (0.02) |
| *Dromius sigma* | ad | 0.02 (0.02) | 0.04 (0.03) | 0.07 (0.06) | 0.02 (0.02) | 0 | 0.03 (0.02) | 0 | 0.02 (0.01) | 0.04 (0.02) |
| Carabidae sp. | l | 0 | 0.01 (0.01) | 0 | 0 | 0 | + | 0 | + | + |
| Carabidae, total | l | 1.87 | 0.93 | 0.45 | 0.49 | 0.42 | 0.83 (0.28) | 0.69 (0.22) | 0.78 (0.20) | 1.38 (0.35) |
| Carabidae, total | ad | 3.94 | 2.85 | 4.13 | 1.00 | 0.65 | 2.52 (0.73) | 0.24 (0.10) | 1.76 (0.49) | 3.09 (0.86) |
| Carabidae, total | l+ad | 5.81 | 3.78 | 4.58 | 1.49 | 1.07 | 3.35 (0.91) | 0.93 (0.23) | 2.54 (0.61) | 4.46 (1.07) |

Table 28. Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) and annual respiration (kcal $m^{-2}$) of Staphylinidae in 1971–72. Standard error is given within parentheses below the corresponding mean value. + denotes a value less than 0.005.
ad = adults l = larvae p = pupae

| | | Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) | | | | | | | | Annual respiration (kcal $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|---|
| | | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual | |
| *Pycnoglypta lurida* | ad | 0 | 0 | 0.08 (0.08) | 0.07 (0.07) | 0.09 (0.09) | 0.05 (0.02) | 0 | 0.03 (0.02) | 0.05 (0.03) |
| *Olophrum assimile* | ad | 0 | 0.37 (0.25) | 0.16 (0.16) | 0 | 0 | 0.11 (0.08) | 0 | 0.07 (0.05) | 0.12 (0.09) |
| *Stenus clavicornis* | ad | 0.12 (0.09) | 0.14 (0.14) | 0.09 (0.06) | 0.05 (0.05) | 0.02 (0.02) | 0.09 (0.03) | 0 | 0.06 (0.02) | 0.10 (0.03) |
| *Stilicus rufipes* | ad | 0.04 (0.04) | 0 | 0 | 0 | 0 | 0.01 (0.01) | 0 | 0.01 (0.01) | 0.01 (0.01) |
| *Lathrobium punctatum* | ad | 0 | 0 | 0 | 0.03 (0.03) | 0 | 0.01 (0.01) | 0.03 (0.03) | 0.02 (0.02) | 0.03 (0.03) |
| *L. geminum* | ad | 0 | 0 | 0 | 0 | 0.03 (0.03) | 0.01 (0.01) | 0 | + | 0.01 (0.01) |
| *L. fulvipenne* | ad | 0.45 (0.33) | 0.27 (0.16) | 0.14 (0.11) | 0.07 (0.07) | 0 | 0.19 (0.08) | 0.13 (0.05) | 0.17 (0.06) | 0.29 (0.10) |
| *L. longulum* | ad | 0 | 0 | 0 | 0 | 0 | 0 | 0.01 (0.01) | + | 0.01 (0.01) |
| *Xantholinus linearis* | ad | 0.07 (0.05) | 0 | 0.04 (0.04) | 0 | 0 | 0.02 (0.02) | 0 | 0.01 (0.01) | 0.03 (0.02) |
| *Othius melanocephalus* | ad | 0.10 (0.08) | 0.02 (0.02) | 0.08 (0.06) | 0.10 (0.08) | 0.09 (0.06) | 0.08 (0.02) | 0.01 (0.01) | 0.05 (0.01) | 0.09 (0.02) |
| *O. lapidicola* | ad | 0 | 0.07 (0.05) | 0.20 (0.13) | 0.02 (0.02) | 0 | 0.06 (0.04) | 0 | 0.04 (0.03) | 0.07 (0.05) |
| *Philonthus varius* | ad | 0 | 0 | 0.05 (0.05) | 0 | 0 | 0.01 (0.01) | 0 | 0.01 (0.01) | 0.01 (0.01) |
| *Staphylinus fuscatus* | ad | 0.24 (0.24) | 0 | 0 | 0 | 0 | 0.05 (0.05) | 0.03 (0.03) | 0.04 (0.04) | 0.08 (0.06) |
| *Quedius fuliginosus* | ad | 0 | 0 | 0.17 (0.17) | 0 | 0 | 0.03 (0.03) | 0 | 0.02 (0.02) | 0.04 (0.04) |
| *Q. curtipennis* | ad | 0 | 0 | 0.77 (0.52) | 0.68 (0.39) | 0.18 (0.18) | 0.33 (0.17) | 0.05 (0.05) | 0.23 (0.12) | 0.41 (0.20) |
| *Q. picipennis* | ad | 0 | 0 | 0.21 (0.21) | 0 | 0 | 0.04 (0.04) | 0 | 0.03 (0.03) | 0.05 (0.05) |
| *Q. fulvicollis* | ad | 0.16 (0.07) | 0.14 (0.08) | 0.45 (0.24) | 0.21 (0.06) | 0.08 (0.06) | 0.21 (0.07) | 0.05 (0.03) | 0.16 (0.05) | 0.27 (0.08) |
| *Mycetoporus splendidus* | ad | 0 | 0 | 0 | 0.07 (0.07) | 0 | 0.01 (0.01) | 0 | 0.01 (0.01) | 0.02 (0.02) |
| *Conosoma pedicularium* | ad | 0 | 0 | 0 | 0.05 (0.05) | 0.03 (0.03) | 0.02 (0.01) | 0.05 (0.03) | 0.03 (0.02) | 0.05 (0.03) |
| *Tachyporus chrysomelinus* | ad | 0.15 (0.06) | 0.12 (0.06) | 0.23 (0.10) | 0.09 (0.06) | 0.06 (0.05) | 0.13 (0.03) | 0.02 (0.02) | 0.09 (0.02) | 0.17 (0.04) |
| *T. pulchellus* | ad | 0.02 (0.02) | 0 | 0 | 0 | 0 | + | 0 | + | + |
| *Tachinus rufipes* | ad | 0.26 (0.16) | 0.14 (0.11) | 0 | 0.02 (0.02) | 0 | 0.09 (0.06) | 0 | 0.06 (0.04) | 0.10 (0.06) |
| *T. rufipennis* | ad | 0 | 0 | 0.10 (0.10) | 0 | 0 | 0.02 (0.02) | 0 | 0.01 (0.01) | 0.02 (0.02) |
| *T. corticinus* | ad | 0.02 (0.02) | 0 | 0 | 0 | 0.15 (0.10) | 0.03 (0.03) | 0.05 (0.05) | 0.04 (0.03) | 0.07 (0.05) |
| *Myllaena minuta* | ad | 0 | 0 | 0 | 0 | 0 | 0 | + | + | + |
| *Schistoglossa gemina* | ad | 0 | 0 | 0.08 (0.04) | 0 | 0 | 0.02 (0.02) | 0 | 0.01 (0.01) | 0.02 (0.02) |
| *Amischa analis* | ad | 0 | 0.04 (0.04) | 0.11 (0.06) | 0.06 (0.04) | 0.02 (0.02) | 0.05 (0.02) | 0.03 (0.02) | 0.04 (0.02) | 0.07 (0.03) |
| *A. cavifrons* | ad | 0 | 0.13 (0.07) | 0.35 (0.14) | 0.23 (0.10) | 0.10 (0.05) | 0.16 (0.06) | 0.22 (0.06) | 0.19 (0.05) | 0.32 (0.08) |
| *Sipalia circellaris* | ad | 0 | 0 | 0.04 (0.04) | 0.07 (0.07) | 0.05 (0.05) | 0.03 (0.02) | 0.03 (0.02) | 0.03 (0.01) | 0.05 (0.02) |
| *Atheta britteni* | ad | 0 | 0 | 0 | 0.03 (0.03) | 0 | 0.01 (0.01) | 0.09 (0.03) | 0.03 (0.01) | 0.06 (0.02) |
| *A. fungi* | ad | 0.10 (0.07) | 0.10 (0.07) | 0.17 (0.10) | 0.36 (0.11) | 0.29 (0.12) | 0.21 (0.06) | 0.18 (0.08) | 0.20 (0.05) | 0.35 (0.08) |
| *Oxypoda advena* | ad | 0 | 0 | 0.10 (0.07) | 0 | 0.03 (0.03) | 0.02 (0.02) | 0 | 0.02 (0.02) | 0.03 (0.03) |
| *O. soror* | ad | 0 | 0 | 0.04 (0.04) | 0 | 0 | 0.01 (0.01) | 0 | 0.01 (0.01) | 0.01 (0.01) |
| *Aleochara brevipennis* | ad | 0 | 0.23 (0.23) | 0 | 0 | 0 | 0.05 (0.05) | 0.13 (0.09) | 0.08 (0.05) | 0.13 (0.08) |
| Staphylinidae, total | ad | 1.74 | 1.78 | 3.65 | 2.20 | 1.21 | 2.12 (0.42) | 1.12 (0.21) | 1.78 (0.29) | 3.13 (0.50) |
| Staphylinidae | l | 0.19 (0.13) | 0.90 (0.60) | 1.73 (0.90) | 3.47 (1.57) | 4.77 (2.25) | 2.21 (0.85) | 1.06 (0.27) | 1.83 (0.57) | 3.21 (1.00) |
| Staphylinidae | p | 0 | 0.42 (0.27) | 0.03 (0.03) | 0 | 0 | 0.09 (0.09) | 0 | 0.06 (0.06) | 0.11 (0.10) |
| Staphylinidae, total | l+p+ad | 1.93 | 3.10 | 5.41 | 5.68 | 5.98 | 4.42 (0.81) | 2.18 (0.36) | 3.67 (0.55) | 6.45 (0.97) |

Table 29. Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) and annual respiration (kcal $m^{-2}$) of soil- or surface-dwelling Coleoptera not belonging to Carabidae or Staphylinidae in 1971–72. This is also given for total Coleoptera. Standard error is given within parentheses below the corresponding mean value. + denotes a value less than 0.005.
ad = adults l = larvae p = pupae

| | | Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) | | | | | | | | Annual respiration (kcal $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|---|
| | | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual | |
| *Megasternum boletophagum* | l | 0 | 0.03 (0.03) | 1.41 (0.49) | 0.97 (0.43) | 0.37 (0.11) | 0.55 (0.28) | 0.52 (0.08) | 0.54 (0.19) | 0.95 (0.33) |
| *M. boletophagum* | ad | 0 | 0 | 0.43 (0.24) | 0.45 (0.25) | 0.18 (0.10) | 0.21 (0.10) | 0.13 (0.06) | 0.19 (0.07) | 0.33 (0.12) |
| *Choleva angustata* | ad | 0 | 0 | 0 | 0 | 0.03 (0.03) | 0.01 (0.01) | 0 | + | 0.01 (0.01) |
| Cantharidae sp. | l | 1.35 (0.90) | 0.02 (0.01) | 0.14 (0.12) | 0.42 (0.28) | 0.15 (0.15) | 0.42 (0.25) | 0.08 (0.08) | 0.30 (0.17) | 0.53 (0.29) |
| *Corymbites aeneus* | l | 0 | 0 | 0.05 (0.05) | 0 | 0 | 0.01 (0.01) | 0 | 0.01 (0.01) | 0.01 (0.01) |
| *Agriotes lineatus/obscurus* | l | 3.41 (0.98) | 4.00 (1.09) | 1.08 (0.47) | 1.59 (0.63) | 0.42 (0.23) | 2.10 (0.69) | 0.65 (0.21) | 1.62 (0.47) | 2.84 (0.82) |
| *Atomaria analis* | ad | 0 | 0 | 0 | 0.09 (0.06) | 0 | 0.02 (0.02) | 0 | 0.01 (0.01) | 0.02 (0.02) |
| *A. atricapilla* | ad | 0.03 (0.03) | 0.08 (0.08) | 0 | 0.40 (0.25) | 0.12 (0.06) | 0.13 (0.08) | 0.15 (0.08) | 0.14 (0.06) | 0.24 (0.10) |
| *Corticaria impressa* | ad | 0 | 0 | 0 | 0.04 (0.04) | 0 | 0.01 (0.01) | 0 | 0.01 (0.01) | 0.01 (0.01) |
| *Corticarina fuscula* | ad | 0 | 0 | 0 | 0 | 0 | 0 | 0.01 (0.01) | + | + |
| *Lagria hirta* | l | 0.04 (0.04) | 0.01 (0.01) | 1.45 (0.58) | 1.59 (1.13) | 0.07 (0.05) | 0.63 (0.37) | 0.14 (0.08) | 0.47 (0.25) | 0.82 (0.43) |
| *Phyllobius piri* | l+p | 20.50 (3.47) | 0 | 56.68 (9.43) | 10.61 (1.34) | 4.71 (1.20) | 18.50 (10.14) | 3.81 (0.73) | 13.60 (6.77) | 23.90 (11.89) |
| *P. viridicollis* | l+p | 2.07 (0.68) | 0 | 0.59 (0.15) | 1.22 (0.21) | 2.06 (0.49) | 1.19 (0.41) | 1.28 (0.21) | 1.22 (0.28) | 2.14 (0.49) |
| Curculionidae sp. | l | 0 | 0 | 0 | 0 | 0 | 0 | 0.01 (0.01) | + | + |
| Coleoptera sp. | l | 0 | 0.15 (0.08) | 0.07 (0.07) | 0 | 0 | 0.04 (0.03) | 0.01 (0.01) | 0.03 (0.02) | 0.05 (0.04) |
| Coleoptera sp. | p | 0 | 0 | 0 | 0.12 (0.12) | 0 | 0.02 (0.02) | 0 | 0.02 (0.02) | 0.03 (0.03) |
| Total of species above | l+p+ad | 27.40 | 4.28 | 61.90 | 17.50 | 8.10 | 23.84 (10.33) | 6.79 (0.77) | 18.15 (6.89) | 31.89 (12.10) |
| Coleoptera, total | l+p+ad | 35.14 | 11.16 | 71.89 | 24.67 | 15.15 | 31.60 (10.90) | 9.89 (0.92) | 24.37 (7.27) | 42.80 (12.77) |

## Discussion

### Abundance

Different separation methods were used in obtaining the abundance estimates. The abundance of the dominant species *Phyllobius piri* was, for example, estimated by means of hand sorting. This method caused an underestimation of less than 15 % of pupae and instar V larvae of *P. piri* according to Axelsson *et al.* (1973a) and since none of the main samplings were performed at times when the larvae were smaller, this degree of reliability was assumed to be valid for all sampling occasions. The reliability of the hand sorting was probably lower for smaller individuals belonging to other species. The gradually increasing estimates of *P. viridicollis* throughout the autumn may be explained by a successively increasing sorting efficiency owing to increasing body size. In reality, the population must have been reduced by mortality ever since the hatching in July (cf. Axelsson *et al.*, 1973a). The *Agriotes* species certainly

also suffered from the inefficient hand sorting, since small (2–8 cm body length) individuals were found at a much lower density than expected from the size-class distributions obtained by other methods (e.g. Salt & Hollick, 1944). In the present study the alternative extraction methods were not reliable for *Agriotes* spp., since the depths of the macroarthropod soil cores for Tullgren funnel extraction were too shallow, and the microarthropod cores for high gradient extraction had too small a surface area. The surface-dwelling Coleoptera, such as many Staphylinidae, were probably extracted reliably in Tullgren funnels, but since this method was not used in May, the estimates for surface-living Staphylinidae on that occasion also had to be based on hand sorting, causing the estimates of smaller specimens belonging to *Amischa* and *Atheta*, among others, to be too low (cf. Table 22).

According to Table 23 the abundance of total Coleoptera fluctuated seasonally with a minimum of about 750 $m^{-2}$ in June and a maximum of about 2200 $m^{-2}$ in September. The number of Coleoptera less *P. piri* and *P. viridicollis* was 1100 (*s.e.* = 320) $m^{-2}$ at the additional sampling on August 4 according to high gradient canister extraction. Furthermore, Axelsson *et al.* (1973a) estimated the *P. piri* population to be 1540 (*s.e.* = 196) and the *P. viridicollis* population to be 165 (*s.e.* = 45) individuals $m^{-2}$ on 9 August 1971 by means of hand sorting. Consequently, the early August density would be about 2800 individuals $m^{-2}$. With regard to the dominance by the two *Phyllobius* species that both hatched in July the real density peak of Coleoptera could be assumed to have occurred in July.

The abundance fluctuations of total Coleoptera greatly depended on the life strategies shown by the dominant species. Both *P. piri* and *P. viridicollis* completed their life cycles within one year, and the abundance low of total Coleoptera on June 15 reflects the absence of these species in the soil due to the earlier emergence of imagines. Other species that emerged from the soil as adults were *Lagria hirta* and the Cantharidae and Elateridae species. The population fluctuations of the *Agriotes* species could not be evaluated thoroughly owing to the inefficient hand sorting, but they were probably small since the generations overlapped as a result of developmental times of 4–5 years in the larval stage (e.g. Guéniat, 1937; Nilsson, 1971). The low abundances did not permit any detailed analysis of the population fluctuations and generation times of the Carabidae species. The most abundant carabid, *Calathus melanocephalus*, had the highest adult estimate in September, while the larvae were most abundant in late autumn and winter. This is in agreement with the findings of other authors, who have classified *C. melanocephalus* as an autumn breeder which predominantly hibernates in the larval stage (Schjøtz-Christensen, 1965; Larsson, 1968).

The abundances of 750–2800 $m^{-2}$ of the total below-ground Coleoptera at Spikbole are some of the higher estimates reported for soil-living Coleoptera. Higher abundances were recorded by Salt *et al.* (1948), who found 3400 $m^{-2}$ in a May sampling and 4400 $m^{-2}$ in a November sampling in an English pasture dominated by Elateridae larvae. Curry (1969) reported an annual mean of 600 $m^{-2}$ in a grassland soil in Ireland. Lower abundances have been found in different steppe habitats in the USSR, from which Ghilarov & Chernov (1974) reported abundances of 70–165 $m^{-2}$, and in tundra grasslands where Bengtsson *et al.* (1974), Chernov *et al.* (1975) and Østbye *et al.* (1975) found a range of 2–290 individuals $m^{-2}$ of total Coleoptera. Most census data concern limited groups of Coleoptera, especially species and families that are important pests on different crops. Bevan (1962) found

September abundances of 30–1400 $m^{-2}$ of the root-feeding larvae of *P. piri* in various grasslands in England, where severe damage was recorded on one-year-old *Agropyron repens* at population levels of 1000–1400 larvae $m^{-2}$. The *P. piri* population at Spikbole was about 800 $m^{-2}$ in September 1971, but no apparent damage was observed on the *A. repens* plants despite the high density. However, younger grass swards are likely to suffer more serious damage than older ones at similar densities of *P. piri* (Bevan, 1962). The annual mean density of about 20 $m^{-2}$ of *Agriotes* larvae at Spikbole falls within the range of 5–100 $m^{-2}$ of Elateridae larvae which is often recorded in grassland soils when estimated by hand sorting (Salt & Hollick, 1944; Dunger, 1968; Dobrovolsky, 1970; Nowak, 1971). Considerably higher densities have been found by flotation methods that are more efficient than hand sorting in estimating the numbers of small-sized larvae. Populations up to 2500 $m^{-2}$ of *Agriotes* larvae were estimated in this way by Salt & Hollick (1944) in English grassland soils. Literature data as well as the results from the present study indicate that non-herbivorous Coleoptera seldom exceed a density of 1000–1500 $m^{-2}$ in temperate grassland soils. Higher abundances usually coincide with high numbers of root-feeding forms, and peak abundances are often associated with the occurrence of damage to the grass sward.

**Biomass**

The hand sorting method favours the recovery of large specimens, which have the greatest contribution to the biomass. The biomasses of, for example, Elateridae larvae and Carabidae were, consequently, more reliably estimated in this study than the corresponding abundances. The annual mean biomass of nearly 3000 mg dw $m^{-2}$ of total Coleoptera and 620 mg dw $m^{-2}$ of Coleoptera less *P. piri* at Spikbole are, hence, considered to be fairly reliable with an underestimation in the region of 10–20 % of the real biomass. The biomass figures from Spikbole are higher than those given by Macfadyen (1963), who estimated the annual mean biomass of the total Coleoptera fauna in an English meadow to be 1100 mg fw $m^{-2}$ which approximates 300 mg dw $m^{-2}$. The annual mean of 230 mg dw $m^{-2}$ of Elateridae larvae at Spikbole is very similar to the estimate of 219 mg dw $m^{-2}$ of Elateridae larvae in a Polish pasture (Kajak, 1974), but considerably lower than the estimate of 850 mg dw $m^{-2}$ in a Polish sheep-fold (Kajak, *op. cit.*).

**Respiration**

The relationship between oxygen consumption rate and live body weight of some Coleoptera groups were calculated from the fairly small number of determinations reported in the literature (see above). Consequently, the relationships calculated must be considered as very tentative. The respiration estimates of larvae and pupae of *P. piri* were based on more relevant data, since both Larsson (unpubl.) and Larsson & Lohm (1975) used larval and pupal material of *P. piri* from Spikbole. The field respiration of pupae was extrapolated from laboratory determinations of respiration rates. This adjustment seemed to be fairly accurate in this case, since the estimate of respired energy based on the laboratory determinations, 7 cal $ind^{-1}$ during the pupal stage, was not far from the independent estimate of energy loss of pupal tissue, 5 (*s.e.* = 0.75) cal $ind^{-1}$, determined on samples of pupae from the field (Larsson & Lohm, 1975).

The annual respiration of about 40 kcal $m^{-2}$ $yr^{-1}$ of below-ground Coleoptera seems

to be very high in view of other respiration studies. Thus, Macfadyen (1963) reported a figure of 9.4 kcal $m^{-2}$ $yr^{-1}$ in a grazed meadow in England, and Satchell (pers. comm.) reported 6.5 kcal $m^{-2}$ $yr^{-1}$ in a deciduous forest in England. However, with regard to the large populations of, for example, *Phyllobius piri* (Bevan, 1962), *Agriotes* spp. (Salt & Hollick, 1944; Salt *et al.*, 1948) and different Scarabaeidae (e.g. Raw, 1967) in some temperate grasslands, the Coleoptera respiration in such localities could be in excess of the estimate at Spikbole.

**Feeding habits**

The feeding habits of Coleoptera are very variable and can differ considerably within the same family and the same species. Most of the Carabidae species are predators both as larvae and adults although omnivory is widely distributed among the imagines (Tischler, 1965). Most species of *Amara* and *Harpalus* seem to be adapted to a prevailingly phytophagous habit both as larvae and imagines, and many *Amara* species feed on grass and herb seeds (Tischler, *op. cit.*). The majority of Staphylinidae are free-living predators during the whole of their life cycles (Wallwork, 1970), e.g. *Stenus, Xantholinus, Philonthus* (Tischler, *op. cit.*), *Tachyporus* and *Tachinus* (Tischler, *op. cit.*; Lipkow, 1966), but there are many exceptions. Some *Aleochara* larvae live, for example, as ectoparasites in the puparia of Diptera Cyclorrhapha (Palm, 1972b). Other species, for example *Oxypoda* spp., *Amischa analis* and *Atheta fungi* are considered to be omnivorous or saprovorous (Tischler, 1965; Wallwork, 1976). The larvae of the elaterids *Agriotes* spp. and *Corymbites (Selatosomus) aeneus* L. are predominantly root feeders, although *Agriotes* also have a tendency towards saprovory (Dunger, 1964; Nilsson, 1971). Also the *Phyllobius* larvae are rhizophagous while, for example, the Cantharidae larvae are known to be carnivorous (Tischler, *op. cit.*).

The classification into main feeding categories was considerably generalized in relation to the diversified feeding habits. Elateridae and Curculionidae larvae were regarded as below-ground herbivores. Adult *Amara* and *Harpalus* were classified as above-ground herbivores, while other carabids were considered as below-ground carnivores. All Staphylinidae and larvae of Cantharidae, *Megasternum, Lagria* and Coleoptera sp. were included in the carnivore category. Adults of *Megasternum, Choleva, Atomaria* and the lathridiids *Corticaria* and *Corticarina* were classified as saprovores/microbivores. The pupae were classified in accordance with the feeding habits of the larvae.

# HYMENOPTERA

## Background

The order Hymenoptera is well represented in the soil. Most data on soil-inhabiting Hymenoptera concern Formicidae and other ant families. Abundance and biomass of ants have been estimated by several investigators (cf. Brian, 1971; Pętal, 1974; Nielsen & Jensen, 1975).

## Methods

Tullgren funnel extraction was used for estimating the population characteristics of adult Hymenoptera Parasitica, but since this type of extraction was not used in May, and since other methods were not suitable, "summer" and annual means were based on only four "summer" samplings (cf. Table 30). A limited number of individuals were weighed collectively, and the mean dry body weight was found to be 0.02 mg. The live body weight was assumed to be 0.08 mg. The mean weights were used to calculate the biomasses and respiratory rates of the parasitic Hymenoptera.

The estimates of adult Formicidae based on Tullgren funnel extraction and hand sorting did not differ over the annual period, but the hand sorting method was preferred because it was also used in May. The ants were weighed individually to the nearest 0.01 mg.

Because of the lack of empirical data, the oxygen consumption rates of Hymenoptera Parasitica were calculated according to the equation given for Collembola, i.e. $Q = 63 \cdot W^{0.73}$ at +18°C, where $Q$ denotes $mm^3$ $O_2$ $ind^{-1}$ $h^{-1}$ and $W$ denotes g mean live body weight. The rates were corrected to the field temperature according to a $Q_{10} = 2.6$ between +18 and +3°C and a $Q_{10} = 3.6$ between +3°C and −2°C (cf. Collembola, p. 57).

The oxygen consumption rates of the ants *Myrmica ruginodis* Nyl. and *M. scabrinodis* Nyl. were calculated according to the relationship between oxygen consumption and body weight given by Jensen & Nielsen (1975) for nine ant species. This relationship was $Q = 625.9 \cdot W^{1.0119}$ at +25°C when presented in a form similar to that of Hymenoptera Parasitica, and assuming the dry body weight to be 30 % of live body weight. The $Q_{10}$ was calculated to be 3.10 between +25 and +5°C by Jensen & Nielsen (*op. cit.*), and this value was also used in the present study assuming an exponential relationship. The $Q_{10}$ was assumed to be 4 below +5°C.

## Results

Twenty-three species of Hymenoptera Parasitica and four species of Formicidae were found in soil cores and emergence traps at Spikbole (cf. Appendix 2), but the numbers of species were certainly much higher, at least in the case of parasitic Hymenoptera. Adult Hymenoptera Parasitica and Formicidae were generally found in the litter and uppermost soil. No juvenile forms of Hymenoptera Parasitica or Formicidae were extracted, but these more or less immobile forms can hardly be extracted by dynamic methods.

The abundance of adult Hymenoptera Parasitica was generally in the region of 100

Table 30. Abundance (no. $m^{-2}$) of Hymenoptera Parasitica and Formicidae in 1971–72. The "summer" and annual means of the former taxon are based on only four "summer" samplings. Standard error is given within parantheses below the corresponding mean value.
n.e. = not estimated T = Tullgren funnel extraction H = Hand sorting

| | | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|
| *Aphaereta* sp. | (T) | n.e. | 5.3 (5.3) | 0 | 0 | 0 | 1.3 (1.3) | 0 | 0.9 (0.9) |
| *Tetramesa* sp. | (T) | n.e. | 53.2 (27.5) | 0 | 0 | 0 | 13.3 (6.9) | 4.3 (4.3) | 10.3 (4.8) |
| *Arescon* sp. | (T) | n.e. | 0 | 0 | 0 | 0 | 0 | 1.8 (1.8) | 0.6 (0.6) |
| ? *Anaphes* sp. | (T) | n.e. | 0 | 5.3 (5.3) | 0 | 0 | 1.3 (1.3) | 0 | 0.9 (0.9) |
| *Aphytis* sp. | (T) | n.e. | 0 | 5.3 (5.3) | 0 | 0 | 1.3 (1.3) | 0 | 0.9 (0.9) |
| Eulophidae sp. | (T) | n.e. | 26.6 (11.9) | 5.3 (5.3) | 0 | 0 | 8.0 (6.4) | 0 | 5.3 (4.3) |
| Encyrtidae sp. | (T) | n.e. | 10.6 (7.1) | 0 | 0 | 0 | 2.7 (1.8) | 0 | 1.8 (1.2) |
| Pteromalidae sp. | (T) | n.e. | 0 | 0 | 5.3 (5.3) | 0 | 1.3 (1.3) | 23.1 (21.4) | 8.6 (7.2) |
| *Spilomicrus basalyformis* | (T) | n.e. | 0 | 0 | 0 | 0 | 0 | 1.8 (1.8) | 0.6 (0.6) |
| *S.* cf. *flavipes* | (T) | n.e. | 0 | 0 | 0 | 0 | 0 | 1.8 (1.8) | 0.6 (0.6) |
| *Trichopria aptera* | (T) | n.e. | 0 | 5.3 (5.3) | 10.6 (7.1) | 0 | 4.0 (2.6) | 3.6 (3.6) | 3.9 (2.1) |
| *T. nigra* | (T) | n.e. | 0 | 0 | 0 | 0 | 0 | 4.3 (4.3) | 1.4 (1.4) |
| *Zygota nigra* | (T) | n.e. | 0 | 5.3 (5.3) | 0 | 0 | 1.3 (1.3) | 0 | 0.9 (0.9) |
| *Gryon* sp. | (T) | n.e. | 5.3 (5.3) | 0 | 0 | 0 | 1.3 (1.3) | 6.1 (4.7) | 2.9 (1.8) |
| *Trimorus* sp. | (T) | n.e. | 0 | 16.0 (8.2) | 0 | 0 | 4.0 (2.1) | 17.5 (7.5) | 8.5 (2.9) |
| *Conostigmus* sp. | (T) | n.e. | 5.3 (5.3) | 5.3 (5.3) | 5.3 (5.3) | 26.6 (11.9) | 10.6 (5.4) | 1.8 (1.8) | 7.7 (3.6) |
| *Lagynodes* sp. | (T) | n.e. | 5.3 (5.3) | 0 | 5.3 (5.3) | 5.3 (5.3) | 4.0 (1.4) | 1.8 (1.8) | 3.3 (1.1) |
| *Ceraphron* sp. | (T) | n.e. | 5.3 (5.3) | 21.3 (14.2) | 79.8 (57.4) | 69.2 (42.8) | 43.9 (18.1) | 43.5 (20.4) | 43.8 (13.9) |
| *Amblyaspis* sp. | (T) | n.e. | 0 | 10.6 (7.1) | 0 | 0 | 2.7 (1.8) | 0 | 1.8 (1.2) |
| *Pezophycta* sp. | (T) | n.e. | 0 | 5.3 (5.3) | 0 | 0 | 1.3 (1.3) | 0 | 0.9 (0.9) |
| Hymenoptera Parasitica, total | (T) | n.e. | 117 (37) | 85 (27) | 106 (73) | 101 (48) | 102 (6.7) | 111 (46) | 105 (16) |
| *Myrmica ruginodis* | (H) | 0 | 1.1 (1.1) | 2.1 (1.5) | 0 | 0 | 0.6 (0.5) | 1.8 (1.4) | 1.0 (0.6) |
| *M. scabrinodis* | (H) | 1.1 (1.1) | 1.1 (1.1) | 0 | 1.1 (1.1) | 0 | 0.6 (0.3) | 0 | 0.4 (0.2) |
| Formicidae, total | (H) | 1.1 (1.1) | 2.1 (1.5) | 2.1 (1.5) | 1.1 (1.1) | 0 | 1.3 (0.4) | 1.8 (1.4) | 1.5 (0.6) |

Table 31. Biomass (mg dry weight $m^{-2}$) of Hymenoptera Parasitica and Formicidae in 1971–72. The "summer" and annual means are based on only four "summer" samplings for the former taxon. Standard error is given within parentheses below the corresponding mean value.
n.e. = not estimated

| | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|
| Hymenoptera Parasitica, total | n.e. | 2.3 (0.8) | 1.7 (0.6) | 2.1 (1.5) | 2.0 (1.0) | 2.1 (0.2) | 2.2 (1.0) | 2.1 (0.4) |
| *Myrmica ruginodis* | 0 | 0.8 (0.8) | 4.2 (2.9) | 0 | 0 | 1.0 (0.8) | 3.5 (2.7) | 1.8 (1.1) |
| *M. scabrinodis* | 1.4 (1.4) | 0.6 (0.6) | 0 | 1.5 (1.5) | 0 | 0.7 (0.4) | 0 | 0.5 (0.3) |
| Formicidae, total | 1.4 (1.4) | 1.4 (1.0) | 4.2 (2.9) | 1.5 (1.5) | 0 | 1.7 (0.7) | 3.5 (2.7) | 2.3 (1.0) |

Table 32. Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) and annual respiration (kcal $m^{-2}$) of Hymenoptera Parasitica and Formicidae in 1971–72. The "summer" and annual means are based on only four "summer" samplings for the former taxon. Standard error is given within parentheses below the corresponding mean value.
n.e. = not estimated

| | Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) | | | | | | | | Annual respiration (kcal $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|
| | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual | |
| Hymenoptera Parasitica, total | n.e. | 0.087 (0.027) | 0.049 (0.016) | 0.047 (0.033) | 0.030 (0.015) | 0.053 (0.012) | 0.025 (0.011) | 0.044 (0.009) | 0.077 (0.015) |
| *Myrmica ruginodis* | 0 | 0.007 (0.007) | 0.028 (0.019) | 0 | 0 | 0.007 (0.006) | 0.007 (0.006) | 0.007 (0.005) | 0.013 (0.008) |
| *M. scabrinodis* | 0.012 (0.012) | 0.006 (0.006) | 0 | 0.007 (0.007) | 0 | 0.005 (0.003) | 0 | 0.003 (0.002) | 0.006 (0.003) |
| Formicidae, total | 0.012 (0.012) | 0.012 (0.009) | 0.028 (0.019) | 0.007 (0.007) | 0 | 0.012 (0.005) | 0.007 (0.006) | 0.010 (0.004) | 0.018 (0.007) |

individuals $m^{-2}$, and the annual mean abundance was 105 (*s.e.* = 16) $m^{-2}$ (Table 30). *Ceraphron* sp. was the most abundant species with 44 (*s.e.* = 14) $m^{-2}$ as an annual mean, and the family Ceraphronidae (*Conostigmus* sp., *Lagynodes* sp. and *Ceraphron* sp.) accounted for 50 % of the total number of Hymenoptera Parasitica. The annual mean number of Formicidae (*Myrmica* spp.) amounted to 1.5 (*s.e.* = 0.6) $m^{-2}$.

The annual mean biomass of Hymenoptera Parasitica was about 2 mg dw $m^{-2}$ (Table 31), but must be considered as a fairly uncertain estimate because it was based on a common mean weight for all parasitic Hymenoptera. The annual mean biomass of Formicidae was estimated at 2.3 (*s.e.* = 1.0) mg dw $m^{-2}$.

The oxygen consumption rates and annual respiration of Hymenoptera Parasitica and Formicidae are given in Table 32. The annual respiration of these groups was estimated at 0.08 (*s.e.* = 0.02) and 0.02 (*s.e.* = 0.01) kcal $m^{-2}$, respectively.

## Discussion

The estimates of both adult Hymenoptera Parasitica and adult Formicidae are probably underestimates of the real populations. The parasitic Hymenoptera obtained by Tullgren funnel extraction was dominated by apterous forms. The winged forms were able to escape from the extractors by flying. Simple random sampling is only rarely suitable for social insects (Brian, 1971), and the estimates of abundance and biomass of the Formicidae were therefore only rough approximations.

The numbers of Hymenoptera Parasitica at Spikbole were about 2–3 times higher than the numbers reported by Salt *et al.* (1948) in an English pasture. The numbers of Formicidae were, however, much lower than the estimates reported by, for example, Salt *et al.* (*op. cit.*), Pętal *et al.* (1971) in Polish meadows, Pętal (1974) in a Polish pasture, and Nielsen & Jensen (1975) in a Danish *Corynephorus* heath locality. The biomasses of Formicidae were also much lower than those estimated by Pętal *et al.* (*op. cit.*), Pętal (*op. cit.*) and Nielsen & Jensen (*op. cit.*). The annual respiration was considerably lower than that reported by Golley & Gentry (1964) for *Pogonomyrmex badius* Latr. which respired 14.2–47.7 kcal $m^{-2}$ $yr^{-1}$ in an abandoned field in South Carolina. Much higher respiration figures have also been presented by Nielsen & Jensen (1975), who calculated the annual respiration to be 59.0 kcal $m^{-2}$ in a Danish *Corynephorus* heath locality.

Hymenoptera Parasitica were classified as soil animals since the specimens obtained were dominated by litter-dwelling forms which often parasitize soil animals. Members of the dominant family Ceraphronidae are known to use Diptera larvae as hosts, and also other proctotrupoids are parasites on Diptera larvae. *Tetramesa* sp. (Eurytomidae) is phytophagous, but most of the other species found at Spikbole are carnivorous in the larval stage. The feeding habits of adult Hymenoptera Parasitica are less known. Some adults consume nectar and aphid excreta, while others feed on the juices welling up from the wounds caused by oviposition in a parasitized animal (Brinck, 1963). Adult Hymenoptera Parasitica can thus be classified as either herbivores or carnivores. However, the energy dissipated as respiration heat by the adults partly or wholly (for non-feeding forms) originates from larval tissues and, therefore, it was preferred to classify the adult Hymenoptera Parasitica as below-ground carnivores. *Myrmica* spp. are chiefly predators (Pętal, 1967) and have been considered as below-ground carnivores.

## Background

The larvae of Diptera are prominent components of the soil fauna, but as a result of problems of extraction and taxonomy they have often been neglected by soil zoologists (Healey & Russell-Smith, 1971). Therefore, there are relatively few reliable estimates of the abundance of Diptera larvae. They generally seem to fall within the broad range of 100–20 000 m$^{-2}$. Biomasses of 10–40 g fw m$^{-2}$ have been recorded in areas with large Tipulidae and/or Bibionidae populations (Cragg, 1961; Szabo *et al.*, 1967), but most biomass estimates are of the order 0.1–10 g fw m$^{-2}$.

## Methods

The sampling of Diptera larvae was based on the microarthropod, macroarthropod and lumbricid sample units, which is in accordance with the sampling of Coleoptera. Diptera pupae were estimated by means of hand sorting the lumbricid soil cores. After the extractions and hand sortings the larvae and pupae were identified, counted, dried in a vacuum-drier at +60°C and weighed individually to the nearest 0.01 mg. The determination of larvae was primarily made according to Hennig (1948, 1950, 1952), Brauns (1954a), Krivošeina (1962) and Theowald (1967), and the determination of pupae was made according to Brauns (1954b). The identification based on larval and pupal characters was supplemented by rearing larvae from the research plot in the laboratory in order to hatch the adults, which are generally easier to identify. Adults were also collected in emergence traps placed on the research plot. Sweep-nettings were made in order to get further information about the species composition.

The relationship between body weight and oxygen consumption rate of the larvae of *Tipula scripta* Meig. and *T. peliostigma* Schumm. has been described as $Q = 115 \cdot W^{0.52}$ at +20°C where $Q$ denotes mm$^3$ $O_2$ ind$^{-1}$ h$^{-1}$ and $W$ denotes g live body weight (Byzova, 1973). This relationship was used in calculating the oxygen consumption rates of Tipulidae larvae at Spikbole. The temperature dependence of the oxygen consumption rates of Tipulidae larvae may be different for different instars (Byzova, 1973; Hofsvang, 1973), but in this study a $Q_{10} = 2.5$ was used to correct the rates between +20 and +5°C independent of instars. A $Q_{10} = 4$ was used for correction to temperatures below +5°C (cf. Byzova, *op. cit.*; Hofsvang, *op. cit.*; MacLean, 1973).

Relatively few data have been published on the oxygen consumption rates of soil-inhabiting Diptera larvae belonging to other families than Tipulidae. Some of these data are given in Table 33, which shows the rates and the corresponding live body weights of larvae from ten different families. The oxygen consumption rates were corrected to +10°C according to a $Q_{10} = 2.5$, and these values were used to calculate a linear relationship of the form $\log Q = \log a + b \log W$ by means of the method of least squares. The equation obtained for +10°C was $Q = 210 \cdot W^{0.87}$, where $Q$ denotes mm$^3$ $O_2$ ind$^{-1}$ h$^{-1}$ and $W$ denotes g live body weight. This equation was based on only one value per Diptera family in order not to over-represent well-studied species such as *Psychoda* spp. (Solbé & Tozer, 1971) and *Drosophila* spp. (Fourche, 1965; Byzova, 1973). The rates of the early stages of *Psychoda* and *Drosophila* larvae were chosen for having representatives also in very small size classes. The equation obtained was used for calculating the oxygen

Table 33. Oxygen consumption rates of Diptera larvae excluding Tipulidae. The rates are, if necessary, adjusted to +10°C by assuming $Q_{10}$ = 2.5.

| | Live wt (mg) | $mm^3$ $O_2$ $g^{-1}$ $h^{-1}$ | $mm^3$ $O_2$ $ind^{-1}$ $h^{-1}$ | Temp. (°C) | $mm^3$ $O_2$ $ind^{-1}$ $h^{-1}$ at+10°C | Reference |
|---|---|---|---|---|---|---|
| Nematocera | | | | | | |
| Psychodidae (*Psychoda severini*, instar I) | 0.0105 | | 0.0028 | 10 | 0.0028 | Solbé & Tozer (1971) |
| Chironomidae | 0.36 | 2900 | 1.04 | 20 | 0.418 | Byzova (1973) |
| Ceratopogonidae (*Forcipomyia* sp.) | 0.43 | 2030 | 0.87 | 20 | 0.349 | " |
| Bibionidae (*Bibio marci*) | 62 | 180 | 11.16 | 14 | 7.736 | Byzova & Prokopeva (1967) |
| Scatopsidae | 2.3 | 2000 | 4.60 | 20 | 1.840 | Byzova (1973) |
| Sciaridae | 4.5 | 1068 | 4.81 | 20 | 1.922 | " |
| Brachycera | | | | | | |
| Rhagionidae | 8.3 | | 2.51 | 13 | 1.903 | Bornebusch (1930) |
| Syrphidae (*Syritta pipiens*) | 17.2 | 632 | 10.87 | 20 | 4.348 | Byzova (1973) |
| Drosophilidae (*Drosophila melanogaster*) | 0.032 | | 0.2 | 25 | 0.051 | Fourche (1965) |
| Calliphoridae (*Phormia regina*) | 60 | 615 | 36.9 | 10 | 36.9 | Keister & Buck (1961) |

consumption rates per individual of the larvae and pupae of Diptera excluding Tipulidae. The oxygen consumption rates were corrected to the field temperatures according to a $Q_{10}$ = 2.5 between +25 and +5°C and a $Q_{10}$ = 4 below +5°C assuming an exponential relationship. A $Q_{10}$ = 2.5 is in accordance with the results on *Chironomus riparius* Meig. (R.W. Edwards, 1958) and *Bibio marci* L. (Byzova & Prokopeva, 1967) with $Q_{10}$ = 2.6 (between +10 and +20°C) and $Q_{10}$ = 2.34 (between +4.5 and +19°C), respectively. $Q_{10}$ = 4 is equal to the temperature dependence of Tipulidae (see above). The mean live body weight per sampling occasion and taxonomic category was used instead of the individual weight ($W$) in calculating the oxygen consumption rates of both Tipulidae and other Diptera. The live body weight was calculated as 4 times the dry weight (Edwards, 1967).

## Results

### Species composition

Relatively few larvae could be determined to the species or genus level based on larval characters alone. The additional information from laboratory hatching showed that most Tipulidae larvae belonged to *Tipula variipennis* Wied. and the Rhagionidae larvae belonged to *Symphoromyia crassicornis* Panz. The Bibionidae larvae were determined

as *Bibio nigriventris* Hal. The latter identification was also supported by the occurrence of adults in the emergence traps, and adults of *B. nigriventris* were also found in mass swarms after the emergence. Several species of Sciaridae were found in the emergence traps, but larvae of this family were not identified to the genus or species level. At least two Orthocladiinae species and three Cecidomyiidae species were distinguished from each other based on the larval characters, but they were not identified to the species level. Most of the larger Empididae larvae belonged to the *Empis/Ramphomyia*-type according to Hennig (1952). A majority of the larvae designated as Acalyptrata sp. were morphologically uniform, and after culturing and hatching in the laboratory it was evident that most of them belonged to *Stiphrosoma sabulosum* Hal. (Anthomyzidae), whose adults have reduced wings. This species was also found in the emergence traps. All Muscidae sp. larvae belonged to the Phaoniinae-type (including Mydaeinae and Coenosiinae) according to Hennig (1952). Several adults of these subfamilies were caught in the emergence traps or by sweep-nettings. Most of the larvae pooled as Cyclorrhapha sp. were probably *Oecothea fenestralis* Fall. (Heleomyzidae), a species which was reared in the laboratory. Also Anthomyiidae-like larvae were classified as Cyclorrhapha sp.

A total number of 96 Diptera species or other taxa was obtained from the research plot when the species from the sweepings were included. However, it is possible that some of these species might have hatched outside the plot. All species obtained are summarized in Appendix 2, which also shows the classification into sub-orders and other taxa.

**Vertical distribution**

Most of the Diptera larvae were found in the uppermost 5 cm of the soil profile, and some larvae like those of Syrphidae sp., *Stiphrosoma sabulosum* and *Fannia* sp. were always found superficially. The vertical distribution of, for example, Tipulidae, Sciaridae, Rhagionidae, Empididae, Dolichopodidae and Muscidae extended to depths of about 10–20 cm during the "winter". Empididae larvae were occasionally found below 20 cm during the "winter". Seasonal changes in the vertical distribution could not, however, be statistically confirmed due to insufficient number of specimens.

**Abundance**

The abundances of the Diptera species and other taxa are presented in Table 34. The high gradient canister extraction was the only extraction method used at the supplementary August sampling. The surface-living Syrphidae sp., Acalyptrata sp. and *Fannia* sp. were primarily extracted by means of Tullgren funnels, but since no Tullgren funnel extraction was made in May, either high gradient canister data or hand sorting data had to replace the Tullgren funnel data on that occasion. Most Nematocera larvae were too small to be hand sorted, and since they also occurred deeper than 3 cm their abundances were based on high gradient canister extractions. Large Brachycera larvae were hand sorted, while the number of small Empididae/Dolichopodidae larvae was based on high gradient canister extractions.

The most abundant Nematocera larvae belonged to *Bibio nigriventris*, Cecidomyiidae spp., Sciaridae sp. and Orthocladiinae spp. with annual mean densities of 2800 (*s.e.* = = 1600), 770 (*s.e.* = 140), 540 (*s.e.* = 110) and 330 (*s.e.* = 120) individuals $m^{-2}$, respectively (Table 34). The *B. nigriventris* larvae were found in clusters, sometimes with several

Table 34. Abundance (no. $m^{-2}$) of larvae (l) and pupae (p) of Diptera in 1971–72. The August values are not used for calculating "summer" and annual means. Standard error is given within parentheses below the corresponding mean value.
n.e. = not estimated
M = Macfadyen high gradient canister extraction
T = Tullgren funnel extraction
H = Hand sorting

| | | | May 17 | June 15 | Aug 4 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Tipula* sp. | l | (H) | 1.1 (1.1) | 0 | n.e. | 0 | 0 | 4.3 (1.9) | 1.1 (0.9) | 0.5 (0.5) | 0.9 (0.6) |
| Orthocladiinae spp. | l | (M) | 190 (190) | 190 (140) | 62 (62) | 250 (190) | 62 (62) | 620 (350) | 260 (95) | 480 (290) | 330 (120) |
| Ceratopogonidae sp. | l | (M) | 0 | 0 | 62 (62) | 0 | 0 | 0 | 0 | 0 | 0 |
| *Bibio nigriventris* | l | (M) | 680 (680) | 0 | 0 | 10 200 (7 000) | 9 800 (9 800) | 0 | 4 100 (2 400) | 0 | 2 800 (1 600) |
| Mycetophilidae sp. | l | (M) | 0 | 0 | 0 | 0 | 0 | 62 (62) | 12 (12) | 0 | 8.2 (8.2) |
| Sciaridae sp. | l | (M) | 62 (62) | 120 (84) | 120 (120) | 310 (250) | 370 (130) | 310 (180) | 230 (60) | 1 100 (310) | 540 (110) |
| Cecidomyiidae spp. | l | (M) | 680 (310) | 560 (270) | 680 (250) | 860 (450) | 370 (260) | 680 (350) | 630 (82) | 1 000 (360) | 770 (140) |
| Nematocera sp. | p | (H) | 1.1 (1.1) | 0 | n.e. | 0 | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| Nematocera, total | l+p | (M+H) | 1 600 | 860 | 930 | 11 700 | 10 600 | 1 700 | 5 300 (2 400) | 2 700 (700) | 4 400 (1 700) |
| *Symphoromyia crassicornis* | l | (H) | 5.3 (2.6) | 0 | n.e. | 4.3 (1.9) | 4.3 (2.5) | 6.4 (3.8) | 4.1 (1.1) | 1.1 (0.8) | 3.1 (0.8) |
| Tabanidae sp. | l | (H) | 1.1 (1.1) | 5.3 (2.1) | n.e. | 2.1 (2.1) | 0 | 5.3 (3.0) | 2.8 (1.1) | 0.5 (0.5) | 2.0 (0.8) |
| Tabanidae sp. | p | (H) | 0 | 1.1 (1.1) | n.e. | 0 | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| Therevidae sp. | l | (H) | 0 | 0 | n.e. | 2.1 (1.5) | 2.1 (2.1) | 0 | 0.9 (0.6) | 2.7 (1.5) | 1.5 (0.7) |
| "Large" Empididae (> 0.50 mg dw $ind^{-1}$) | l | (H) | 13 (3.9) | 0 | n.e. | 1.1 (1.1) | 12 (4.6) | 8.5 (3.1) | 6.8 (2.7) | 7.0 (2.0) | 6.9 (1.9) |
| Empididae sp. | p | (H) | 3.2 (1.8) | 6.4 (2.7) | n.e. | 2.1 (1.5) | 0 | 0 | 2.4 (1.2) | 0 | 1.6 (0.8) |
| "Large" Dolichopodidae (> 0.50 mg dw $ind^{-1}$) | l | (H) | 3.2 (1.8) | 0 | n.e. | 2.1 (1.5) | 2.1 (2.1) | 6.4 (4.4) | 2.8 (1.1) | 3.8 (2.7) | 3.1 (1.2) |
| "Small" Empididae/Dolichopodidae (< 0.50 mg dw $ind^{-1}$) | l | (M) | 310 (200) | 62 (62) | 800 (260) | 370 (130) | 190 (99) | 62 (62) | 200 (63) | 1 300 (960) | 550 (330) |
| Syrphidae sp. | l | (T+H) | 0 | 0 | n.e. | 0 | 5.3 (5.3) | 5.3 (5.3) | 2.1 (1.3) | 6.1 (4.7) | 3.4 (1.8) |
| Acalyptrata sp. | l | (M+T) | 0 | 37 (16) | 430 (160) | 780 (140) | 1 100 (120) | 660 (120) | 520 (220) | 480 (110) | 510 (150) |
| *Fannia* sp. | l | (M+T) | 0 | 0 | 120 (85) | 37 (23) | 27 (12) | 21 (12) | 17 (7.5) | 22 (9.5) | 19 (5.9) |
| Muscidae sp. | l | (M+H) | 0 | 0 | 62 (62) | 12 (5.8) | 19 (5.3) | 32 (26) | 13 (6.1) | 21 (6.2) | 15 (4.6) |
| Cyclorrhapha sp. | l | (H) | 1.1 (1.1) | 3.2 (2.4) | n.e. | 0 | 5.3 (2.6) | 6.4 (4.4) | 3.2 (1.3) | 19 (13) | 8.6 (4.4) |
| Cyclorrhapha sp. | p | (H) | 6.4 (3.8) | 15 (4.0) | n.e. | 6.4 (4.4) | 0 | 0 | 5.6 (2.8) | 0 | 3.7 (1.9) |
| Brachycera, total | l+p | (M+T+H) | 340 | 130 | 1 400 | 1 200 | 1 400 | 820 | 780 (250) | 1 800 (980) | 1 100 (370) |
| Diptera, total | l+p | (M+T+H) | 1 900 | 990 | 2 300 | 12 900 | 12 000 | 2 500 | 6 100 (2 700) | 4 500 (1 200) | 5 500 (1 800) |

hundred individuals in each, and due to the limited extension in space of these aggregations the soil corer either hit a cluster or no individual at all. This caused a very low precision in the estimates. This extreme form of aggregation was not found for any of the other Nematocera larvae. The annual mean abundance of larvae and pupae of Nematocera was estimated at 4400 (*s.e.* = 1700) $m^{-2}$, of which Nematocera less *B. nigriventris* accounted for 1600 (*s.e.* = 260) $m^{-2}$.

Most of the Brachycera larvae belonged to Empididae and/or Dolichopodidae and to Acalyptrata (Table 34). Small Empididae and Dolichopodidae were difficult to separate during the first larval instars and were therefore pooled. The annual mean number of the larvae and pupae of these two families was about 560 $m^{-2}$, while Acalyptrata sp. with the dominant species *Stiphrosoma sabulosum* amounted to 510 (*s.e.* = 150) larvae $m^{-2}$. The other Brachycera species were much less abundant. The total annual mean abundance of Brachycera larvae and pupae was 1100 (*s.e.* = 370) $m^{-2}$, and the corresponding value of total Diptera was 5500 (*s.e.* = 1800) $m^{-2}$.

The abundance of Nematocera larvae less *B. nigriventris* fluctuated fairly little over the study period, with a range of about 800 to 1700 $m^{-2}$. Larvae belonging to Orthocladiinae, Sciaridae and Cecidomyiidae were found on all sampling occasions, which indicated that the species within each of these families had different phenologies. The "winter" abundance of Nematocera less *B. nigriventris* was about twice that of the "summer" mean. The fluctuation in the number of Brachycera larvae was more pronounced than that of the Nematocera larvae. Only about 100 Brachycera larvae $m^{-2}$ were found in June, while the numbers were of the order 1200–1500 $m^{-2}$ in August, September and October. Obviously the low larval density in June coincided with the pupal and emergence period of many Brachycera species. This was also supported by the information of adult occurrence obtained by emergence traps and sweep nets (cf. Appendix 2). For example, *Empis tesselata* Fabr. and *E. stercorea* L. became adults in June, but Empididae pupae did not only occur in May and June but also in September, implying that some pupae belonged to autumn-emerging empidids such as *Ramphomyia spinipes* Fall. The Acalyptrata species *Stiphrosoma sabulosum* occurred in the soil cores from the early autumn to the winter and emerged in the early June. The same pattern of development was shown by the Muscidae larvae, of which adults of *Mydaea* sp., *Helina* spp. and *Hydrotaea* sp. were caught in the emergence traps in June and July. The highest abundance of total Brachycera was recorded during the "winter" period, which agrees with the data on Nematocera. The high "winter" density was chiefly caused by the "small" Empididae/Dolichopodidae larvae.

**Biomass**

The larvae of *Bibio nigriventris* were estimated to have the highest annual mean biomass of the Nematocera larvae with 230 (*s.e.* = 140) mg dw $m^{-2}$ (Table 35). Other Nematocera species with high biomasses were Sciaridae, Cecidomyiidae and *Tipula* larvae with 59 (*s.e.* = 17), 17 (*s.e.* = 5.8) and 15 (*s.e.* = 12) mg dw $m^{-2}$, respectively. The annual mean biomass of larvae and pupae of total Nematocera was 320 (*s.e.* = 130) mg dw $m^{-2}$, of which the Nematocera larvae less *B. nigriventris* contributed 94 (*s.e.* = 22) mg $m^{-2}$.

The annual mean biomass of Brachycera was dominated by Muscidae, "large" Empididae, *Symphoromyia crassicornis*, Tabanidae and Acalyptrata larvae with 90 (*s.e.* = 30),

Table 35. Biomass (mg dry weight $m^{-2}$) of larvae (l) and pupae (p) of Diptera in 1971–72. The August values are not used for calculating "summer" and annual means. Standard error is given within parentheses below the corresponding mean value. n.e. = not estimated

| | | May 17 | June 15 | Aug 4 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|---|
| *Tipula* sp. | l | 3.4 (3.4) | 0 | n.e. | 0 | 0 | 82.9 (38.4) | 17.2 (16.5) | 10.8 (10.8) | 15.1 (11.6) |
| Orthocladiinae spp. | l | 4.3 (4.3) | 1.9 (1.4) | 4.9 (4.9) | 0.6 (0.6) | 1.2 (1.2) | 2.8 (1.5) | 2.2 (0.7) | 3.3 (1.8) | 2.5 (0.8) |
| Ceratopogonidae sp. | l | 0 | 0 | 4.9 (4.9) | 0 | 0 | 0 | 0 | 0 | 0 |
| *Bibio nigriventris* | l | 558.0 (558.0) | 0 | 0 | 114.8 (78.5) | 1 031.5 (1 031.5) | 0 | 340.9 (201.0) | 0 | 227.2 (134.0) |
| Mycetophilidae sp. | l | 0 | 0 | 0 | 0 | 0 | 1.2 (1.2) | 0.3 (0.3) | 0 | 0.2 (0.2) |
| Sciaridae sp. | l | 7.4 (7.4) | 21.6 (19.2) | 6.2 (6.2) | 4.3 (3.8) | 18.2 (12.3) | 35.8 (26.4) | 17.5 (5.6) | 142.3 (48.1) | 59.1 (16.5) |
| Cecidomyiidae spp. | l | 11.7 (7.5) | 30.3 (15.7) | 45.4 (23.1) | 15.4 (11.8) | 0.9 (0.7) | 2.2 (1.0) | 12.1 (5.3) | 28.2 (13.5) | 17.5 (5.8) |
| Nematocera sp. | p | 1.4 (1.4) | 0 | n.e. | 0 | 0 | 0 | 0.3 (0.3) | 0 | 0.2 (0.2) |
| Nematocera, total | l+p | 586 | 54 | 61 | 135 | 1 052 | 125 | 390 (191) | 185 (52) | 322 (129) |
| *Symphoromyia crassicornis* | l | 30.0 (15.1) | 0 | n.e. | 40.1 (21.5) | 41.0 (26.2) | 81.6 (47.1) | 38.5 (13.1) | 9.5 (8.0) | 28.8 (9.2) |
| Tabanidae sp. | l | 6.4 (6.4) | 84.6 (34.4) | n.e. | 45.6 (45.6) | 0 | 56.3 (41.7) | 38.6 (15.9) | 10.8 (10.8) | 29.3 (11.2) |
| Tabanidae sp. | p | 0 | 5.0 (5.0) | n.e. | 0 | 0 | 0 | 1.0 (1.0) | 0 | 0.7 (0.7) |
| Therevidae sp. | l | 0 | 0 | n.e. | 1.5 (1.3) | 42.2 (42.2) | 0 | 8.7 (8.4) | 11.9 (10.5) | 9.8 (6.6) |
| "Large" Empididae ($>0.50$ mg dry wt $ind^{-1}$) | l | 143.7 (51.2) | 0 | n.e. | 4.0 (4.0) | 73.9 (28.2) | 44.8 (34.3) | 53.3 (26.4) | 73.9 (27.5) | 60.2 (19.9) |
| Empididae sp. | p | 1.9 (1.1) | 30.8 (24.2) | n.e. | 7.4 (5.1) | 0 | 0 | 8.0 (5.9) | 0 | 5.3 (3.9) |
| "Large" Dolichopodidae ($>0.50$ mg dry wt $ind^{-1}$) | l | 8.6 (6.7) | 0 | n.e. | 3.1 (2.4) | 2.1 (2.1) | 31.5 (24.3) | 9.1 (5.8) | 12.7 (8.5) | 10.3 (4.8) |
| "Small" Empididae/Dolichopodidae ($<0.50$ mg dry wt $ind^{-1}$) | l | 25.3 (17.2) | 5.6 (5.6) | 47.8 (21.2) | 11.4 (7.2) | 12.4 (8.6) | 0.3 (0.3) | 11.0 (4.2) | 29.9 (14.5) | 17.3 (5.6) |
| Syrphidae sp. | l | 0 | 0 | n.e. | 0 | 7.6 (7.6) | 19.4 (19.4) | 5.4 (3.8) | 34.3 (27.3) | 15.0 (9.5) |
| Acalyptrata sp. | l | 0 | 1.0 (0.8) | 9.3 (5.1) | 25.0 (5.5) | 44.2 (7.0) | 38.8 (7.3) | 21.8 (9.3) | 35.7 (8.0) | 26.4 (6.7) |
| *Fannia* sp. | l | 0 | 0 | 2.5 (2.0) | 5.7 (3.1) | 8.5 (3.6) | 8.9 (5.0) | 4.6 (2.0) | 18.6 (7.3) | 9.3 (2.8) |
| Muscidae sp. | l | 0 | 0 | 23.5 (23.5) | 35.9 (18.5) | 109.3 (34.8) | 211.3 (148.2) | 71.3 (40.3) | 127.7 (39.7) | 90.1 (30.0) |
| Cyclorrhapha sp. | l | 5.7 (5.7) | 4.9 (3.4) | n.e. | 0 | 14.2 (7.3) | 19.6 (16.0) | 8.9 (3.6) | 39.6 (26.0) | 19.1 (9.0) |
| Cyclorrhapha sp. | p | 15.3 (9.1) | 40.6 (15.1) | n.e. | 15.6 (8.9) | 0 | 0 | 14.3 (7.5) | 0 | 9.5 (5.0) |
| Brachycera, total | l+p | 237 | 172 | 83 | 195 | 355 | 512 | 294 (63) | 405 (81) | 331 (50) |
| Diptera, total | l+p | 823 | 226 | 144 | 330 | 1 407 | 637 | 685 (210) | 589 (106) | 653 (145) |

60 (*s.e.* = 20), 29 (*s.e.* = 9.2), 29 (*s.e.* = 12) and 26 (*s.e.* = 6.7) mg dw $m^{-2}$, respectively. As a whole the annual mean biomass of Brachycera was 330 (*s.e.* = 50) mg dw $m^{-2}$, and the equivalent value for total Diptera was 650 (*s.e.* = 150) mg $m^{-2}$.

The biomasses of the Diptera larvae changed seasonally, the changes being more conspicuous for individual species than for larger taxonomic groups which included species with overlapping development cycles. The biomass fluctuations of the *B. nigriventris* larvae could not be accurately studied by means of the sample sizes and sample units used. The mean dry weights of the *B. nigriventris* larvae were 0.011, 0.11 and 1.2 mg in September, October and May, respectively, which together with the emergence and mass swarming in the middle of June indicated that this species was univoltine with a high biomass in the late autumn, winter and spring. The larvae of Cecidomyiidae seemed to be the only Nematocera family with a biomass maximum during the summer.

The biomass of the total Brachycera larvae fluctuated from about 100 mg dw $m^{-2}$ in June (the August sampling with 83 (*s.e.* = 33) mg $m^{-2}$ was incomplete) to about 500 mg dw $m^{-2}$ in November. The successive increase in biomass during the autumn coincided with an increase in body weight for many species. The mean dry weights of the Muscidae larvae were, for example, 0.4 mg in August (uncertain value), 3.1 mg in September, 5.8 mg in October and 6.6 mg in November, while the mean body weight was 6.1 mg during the "winter" period. The Acalyptrata larvae, most of which were *Stiphrosoma sabulosum*, averaged 0.02, 0.03, 0.04, 0.05 and 0.06 mg dw $ind^{-1}$ in August, September, October, November and the "winter", respectively. The mean weight of "large" Empididae also increased from September (3.7 mg) to the "winter" (10.5 mg), but the highest mean weight of "large" Empididae larvae was found in May (11.2 mg) just before the pupation in May/June. The total biomass of Diptera larvae less *B. nigriventris* was lowest in June and August with about 150 mg dw $m^{-2}$. It increased successively to about 200 in September, 375 in October and 640 mg dw $m^{-2}$ in November. The "winter" value was 590 (*s.e.* = 110) mg dw $m^{-2}$, while the biomass in May was about 250 mg dw $m^{-2}$. The pupal biomass was highest in June with nearly 80 mg dw $m^{-2}$.

**Respiration**

The oxygen consumption rates of larvae and pupae of Diptera and their annual respiration are presented in Table 36. *Bibio nigriventris* had the highest annual respiration with 16 (*s.e.* = 8.5) kcal $m^{-2}$. Other taxa with a high contribution to the Nematocera respiration were Sciaridae and Cecidomyiidae larvae with 2.0 (*s.e.* = 0.5) and 1.2 (*s.e.* = 0.5) kcal $m^{-2}$, respectively. The annual respiration of Nematocera was 19 (*s.e.* = 8.2) kcal $m^{-2}$, of which the Nematocera species excluding *B. nigriventris* accounted for 3.7 (*s.e.* = 0.4) kcal $m^{-2}$.

Brachycera larvae with high respiration were Muscidae, "large" Empididae, Acalyptrata, Tabanidae and "small" Empididae/Dolichopodidae with 2.1 (*s.e.* = 0.7), 1.9 (*s.e.* = 1.0), 1.3 (*s.e.* = 0.5), 1.1 (*s.e.* = 0.6) and 1.0 (*s.e.* = 0.4) kcal $m^{-2}$ $yr^{-1}$. The annual respiration of larvae and pupae of Brachycera was 11 (*s.e.* = 0.8) kcal $m^{-2}$. As a whole the larvae and pupae of Diptera respired 30 (*s.e.* = 8.8) kcal $m^{-2}$. Total Diptera excluding *B. nigriventris* accounted for 15 (*s.e.* = 0.9) kcal $m^{-2}$ $yr^{-1}$.

The oxygen consumption rates of Brachycera and total Diptera excluding *B. nigri-*

Table 36. Oxygen consumption rates ($cm^3$ $O_2$ $ind^{-1}$ $h^{-1}$) and the annual respiration (kcal $m^{-2}$) of larvae (l) and pupae (p) of Diptera in 1971–72. The August values are not used for calculating "summer" and annual means. Standard error is given within parentheses below the corresponding mean value. + denotes a value less than 0.005. n.e. = not estimated.

| | | Oxygen consumption rates ($cm^3$ $O_2$ $ind^{-1}$ $h^{-1}$) | | | | | | | | | Annual respiration (kcal $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | May 17 | June 15 | Aug 4 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual | |
| *Tipula* sp. | l | 0.12 (0.12) | 0 | n.e. | 0 | 0 | 0.89 (0.40) | 0.20 (0.18) | 0.08 (0.08) | 0.16 (0.12) | 0.29 (0.21) |
| Orthocladinae spp. | l | 0.30 (0.30) | 0.14 (0.11) | 0.45 (0.45) | 0.05 (0.04) | 0.05 (0.05) | 0.09 (0.05) | 0.13 (0.05) | 0.07 (0.04) | 0.11 (0.04) | 0.19 (0.06) |
| Ceratopogonidae sp. | l | 0 | 0 | 0.45 (0.45) | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Bibio nigriventris* | l | 24.31 (24.31) | 0 | 0 | 6.92 (4.73) | 36.11 (36.11) | 0 | 13.47 (7.20) | 0 | 8.98 (4.80) | 15.77 (8.43) |
| Mycetophilidae sp. | l | 0 | 0 | 0 | 0 | 0 | 0.03 (0.03) | 0.01 (0.01) | 0 | + | 0.01 (0.01) |
| Sciaridae sp. | l | 0.41 (0.41) | 1.15 (0.79) | 0.60 (0.60) | 0.25 (0.21) | 0.71 (0.23) | 0.75 (0.43) | 0.65 (0.16) | 2.15 (0.73) | 1.15 (0.27) | 2.03 (0.47) |
| Cecidomyiidae spp. | l | 0.84 (0.38) | 1.88 (0.91) | 4.21 (1.54) | 0.87 (0.45) | 0.05 (0.04) | 0.07 (0.04) | 0.74 (0.34) | 0.52 (0.25) | 0.67 (0.24) | 1.17 (0.42) |
| Nematocera sp. | p | 0.06 (0.06) | 0 | n.e. | 0 | 0 | 0 | 0.01 (0.01) | 0 | 0.01 (0.01) | 0.01 (0.01) |
| Nematocera, total | l+p | 26.05 | 3.17 | 5.25 | 8.08 | 36.92 | 1.84 | 15.21 (6.94) | 2.83 (0.80) | 11.08 (4.64) | 19.47 (8.15) |
| *Symphoromyia crassicornis* | l | 1.02 (0.49) | 0 | n.e. | 1.00 (0.45) | 0.80 (0.46) | 0.93 (0.55) | 0.75 (0.20) | 0.08 (0.07) | 0.53 (0.13) | 0.93 (0.23) |
| Tabanidae sp. | l | 0.22 (0.22) | 2.51 (0.95) | n.e. | 1.02 (1.02) | 0 | 0.66 (0.37) | 0.88 (0.45) | 0.08 (0.08) | 0.62 (0.30) | 1.08 (0.53) |
| Tabanidae sp. | p | 0 | 0.17 (0.17) | n.e. | 0 | 0 | 0 | 0.03 (0.03) | 0 | 0.02 (0.02) | 0.04 (0.04) |
| Therevidae sp. | l | 0 | 0 | n.e. | 0.05 (0.04) | 0.75 (0.75) | 0 | 0.16 (0.15) | 0.11 (0.10) | 0.14 (0.11) | 0.25 (0.19) |
| "Large" Empididae (> 0.50 mg dry wt $ind^{-1}$) | l | 4.46 (1.36) | 0 | n.e. | 0.11 (0.11) | 1.52 (0.59) | 0.57 (0.21) | 1.33 (0.83) | 0.63 (0.24) | 1.10 (0.56) | 1.93 (0.98) |
| Empididae sp. | p | 0.09 (0.05) | 1.07 (0.44) | n.e. | 0.21 (0.15) | 0 | 0 | 0.27 (0.21) | 0 | 0.18 (0.14) | 0.32 (0.24) |
| "Large" Dolichopodidae (> 0.50 mg dry wt $ind^{-1}$) | l | 0.32 (0.18) | 0 | n.e. | 0.10 (0.07) | 0.06 (0.06) | 0.41 (0.28) | 0.18 (0.08) | 0.13 (0.09) | 0.16 (0.06) | 0.28 (0.11) |
| "Small" Empididae/Dolichopodidae (< 0.50 mg dry wt $ind^{-1}$) | l | 1.49 (0.94) | 0.32 (0.32) | 4.50 (1.43) | 0.60 (0.20) | 0.46 (0.25) | 0.01 (0.01) | 0.58 (0.25) | 0.56 (0.27) | 0.57 (0.19) | 1.00 (0.34) |
| Syrphidae sp. | l | 0 | 0 | n.e. | 0 | 0.19 (0.19) | 0.26 (0.26) | 0.09 (0.06) | 0.32 (0.25) | 0.17 (0.10) | 0.29 (0.16) |
| Acalyptrata sp. | l | 0 | 0.07 (0.03) | 1.00 (0.36) | 1.31 (0.23) | 1.75 (0.19) | 0.89 (0.16) | 0.80 (0.35) | 0.58 (0.13) | 0.73 (0.24) | 1.28 (0.41) |
| *Fannia* sp. | l | 0 | 0 | 0.27 (0.19) | 0.24 (0.15) | 0.26 (0.12) | 0.16 (0.09) | 0.13 (0.06) | 0.22 (0.09) | 0.16 (0.05) | 0.28 (0.09) |
| Muscidae sp. | l | 0 | 0 | 1.74 (1.74) | 1.04 (0.51) | 2.28 (0.62) | 2.62 (2.08) | 1.19 (0.56) | 1.17 (0.37) | 1.18 (0.39) | 2.07 (0.68) |
| Cyclorrhapha sp. | l | 0.19 (0.19) | 0.20 (0.15) | n.e. | 0 | 0.33 (0.16) | 0.26 (0.17) | 0.20 (0.06) | 0.42 (0.28) | 0.27 (0.10) | 0.47 (0.18) |
| Cyclorrhapha sp. | p | 0.58 (0.35) | 1.52 (0.41) | n.e. | 0.46 (0.32) | 0 | 0 | 0.51 (0.28) | 0 | 0.34 (0.19) | 0.60 (0.33) |
| Brachycera, total | l+p | 8.36 | 5.85 | 7.51 | 6.16 | 8.39 | 6.77 | 7.10 (0.54) | 4.29 (0.75) | 6.17 (0.44) | 10.83 (0.77) |
| Diptera, total | l+p | 34.41 | 9.02 | 12.76 | 14.24 | 45.30 | 8.61 | 22.32 (7.44) | 7.12 (1.20) | 17.25 (4.97) | 30.31 (8.74) |

*ventris* fluctuated fairly little over the year. The rates for total Diptera, for example, ranged from 7.1 $cm^3$ $O_2$ $m^{-2}$ $day^{-1}$ during the "winter" to 12.8 $cm^3$ $O_2$ $m^{-2}$ $day^{-1}$ in August.

## Discussion

### Abundance

The efficiency of extracting Diptera larvae by means of simple Tullgren funnels seems to be fairly low. Van der Drift (1951) found that on average only 12 % of the Sciaridae larvae added to animal-free substrate were extracted. However, van der Drift (*op. cit.*) suspected that these larvae were too delicate for such an experiment. Healey & Russell-Smith (1970) compared the efficiencies of simple Tullgren funnels and high gradient canister extractors wich a glycerol-water flotation method. The results indicated that only 12 % of the larvae were extracted in the Tullgren funnels and 26 % in the high gradient canisters in relation to the flotation method, which seemed to be highly efficient. The Tullgren funnels were, however, more efficient in extracting larvae from litter (18 %) than from humus (7 %). The humus sub-cores used by Healey & Russell-Smith (*op. cit.*) for high gradient canister extraction were 3 cm thick, while those from Spikbole were only 2 cm. The thicker sub-cores might have reduced the extraction efficiency, and it is also probable that the extraction of the larvae from Spikbole was promoted by the porous soil structure in comparison with Healey & Russell-Smith's test. Notwithstanding, the combined Tullgren funnel and high gradient canister methods used at Spikbole must have underestimated the population sizes, at least those of some Diptera groups. This is also indicated by the different abundances obtained in August to November on one hand and in the "winter" on the other. The "winter" abundance of Nematocera larvae excluding *Bibio nigriventris* was about twice that found from August to November, although probably no hatching occurred during the late autumn due to the low temperatures. A similar tendency was found for "small" Empididae Dolichopodidae larvae, which were also extracted by means of the high gradient canister method. The apparent increase in abundance from October November to the "winter" was interpreted as caused by an increase in extraction efficiency, mainly due to the frost that maintained the pore structure and prevented soil compression (cf. Collembola, p. 76). Thus, the real number of soil-inhabiting larvae should have been underestimated during the "summer" period (cf. Fig. 25).

Most of the Diptera species do not remain in the soil in the adult stage. Therefore, species that complete their life cycle within one year generally disappear from the soil at certain times. Consequently, the abundances of such species may fluctuate considerably, with maximum larval abundances occurring immediately after the hatching of the eggs. A majority of the species at Spikbole seemed to have life cycles lasting one year or less, and most species appeared to pupate and emerge in the early summer. Only in Cecidomyiidae, Sciaridae, Orthocladiinae, Empididae/Dolichopodidae and possibly Tabanidae and Acalyptrata were there species that diverged from the general pattern. Thus the lowest number of Diptera larvae occurred in June, while the highest number should probably have occurred in the late summer or early autumn, although this was obscured by insufficient extraction of small larvae at that time. Most of the pupae were re-

corded in June. Since the pupae were sorted by hand, reliable estimates were only obtained for the largest species.

There are few published data on the abundance of Diptera larvae in grasslands. Salt *et al.* (1948) estimated the number to be 709 and 672 $m^{-2}$ at a May and a November sampling, respectively, in an English pasture, and Curry (1969) recorded the annual mean abundance to be 1280 $m^{-2}$ in an Irish grassland. The latter value was obtained by high gradient canister extraction and is thus comparable with the annual mean number of 2800 $m^{-2}$ for larvae and pupae of Diptera less *B. nigriventris* and 5500 $m^{-2}$ for Diptera including this species at Spikbole. The annual means at Spikbole seem to be relatively high in spite of the presumed underestimation, but higher values have been reported by Healey & Russell-Smith (1970, 1971), who found an annual mean of 12 150 larvae $m^{-2}$ in a calcareous mull soil in an English woodland.

### Biomass

The biomass of Diptera larvae less *Bibio nigriventris* increased from a low in June and August to a maximum in November, which coincided with the individual growth period of most larvae. The biomass decreased somewhat during the "winter" due to starvation and/or mortality, and fell to half that level in May, presupposing an equal biomass in 1972 as in 1971. Also *B. nigriventris* had a similar development according to the individual weights, but since its last instar larvae probably increased in weight before pupation in May/June the total biomass of Diptera larvae might have retained as high a level in May as during the "winter". The pupae contributed considerably to the Diptera biomass in the early summer and, consequently, it is reasonable to assume that the minimum biomass of the soil- and litter-inhabiting stages of Diptera was reached during the late summer when most pupae had hatched and most larvae were still small (cf. Fig. 25).

The annual mean estimate of total Diptera of 0.65 g dw $m^{-2}$ or 2.6 g fw $m^{-2}$ at Spikbole falls within the range of other grassland estimates. High biomasses have been found in high-altitude grasslands with dense Tipulidae populations. Thus Cragg (1961) reported a (peak?) biomass of 36 g fw $m^{-2}$ for Tipulidae in an upland grassland in England, and Hofsvang (1972) found a peak biomass of about 5 g fresh (?) weight $m^{-2}$ for *Tipula excisa* Schum. in a high mountain tussock field in Norway. Chernov *et al.* (1975) obtained 3.83 g fw $m^{-2}$ of Tipulidae in July in a herb-grass stand in Western Taimyr. Macfadyen (1963) estimated the annual mean biomass of total Diptera to be 1.2 g fw $m^{-2}$ in a grazed meadow in England.

### Respiration

The relationship between oxygen consumption rate ($Q$) and live body weight ($W$) for Diptera larvae excluding Tipulidae was calculated to be $Q = 210 \cdot W^{0.87}$ at +10°C, when based on determinations representing ten Diptera families (cf. Table 33). This relationship is very approximate and the use of one equation for most Diptera larvae may well be questioned since there are considerable differences between the oxygen consumption rates of some species. The rates obtained by Fourche (1965) for *Drosophila melanogaster* L. of different body weights are, for example, 10–20 times higher than those found by Solbé & Tozer (1971) for *Psychoda severini parthenogenetica* Tonn. and *P. alternata* Say, of equivalent weights. However, since more extensive data are lacking,

only one equation was used for Diptera larvae not belonging to Tipulidae. Recently Olechowicz (1976) has presented data on the respiration rates of the coprophagous larvae of the anthomyid *Paregle eastiva* Meig. at +25°C that have not been taken into consideration in Table 33. She estimated the relationship between oxygen consumption rate and live body weight (0.1 -6 mg fw weight range) to be $Q = 460 \cdot W^{0.8025}$ when expressed in the same units as above. According to a $Q_{10} = 2.5$ this equation corresponds to $Q = 116.4 \cdot W^{0.8025}$ at +10°C, which is in close agreement with the equation given above for the weight range concerned.

Diptera larvae living in close aggregations, such as *Bibio marci* L., may affect their ambient temperature considerably. Byzova & Prokopeva (1967) observed that the temperature within a cluster of *B. marci* larvae exceeded that in the surroundings and the oxygen consumption rates for the larvae within the cluster were enhanced in comparison with larvae removed from the aggregation. Consequently, oxygen consumption rates based on mean soil temperatures are underestimates under such circumstances. The larvae of *B. nigriventris* were also found in clusters at Spikbole, but owing to the lack of detailed temperature data, the respiration of these larvae was calculated in the same way as the other Diptera larvae which were more evenly dispersed.

The pupal stage of holometabolous insects is generally characterized by an initial decrease in metabolic activity followed by an intermediate period of low activity and a successive restitution of the metabolism at the end of the stage (Agrell & Lundquist, 1973; Keister & Buck, 1974). This U-shaped curve makes it difficult to predict the respiratory rate in the field when the phase of the pupal development is poorly known. In this study the oxygen consumption rates of Diptera pupae were calculated from the same equation as those of the larvae. The respiratory rates of pupae are generally lower than those of larvae (e.g. Wigglesworth, 1965; Olechowicz, 1976), which might have caused an overestimation of the true rates, but since the hand sorting method certainly led to the number and biomass of the pupae being underestimated, it is impossible to judge whether the annual respiration figures for the pupae were over- or underestimated.

The annual respiration of about 30 kcal $m^{-2}$ $yr^{-1}$ for Diptera larvae and pupae at Spikbole is considerably lower than the figures for a high-altitude limestone grassland (149 kcal $m^{-2}$ $yr^{-1}$) and a high-altitude *Juncus* moor (131 kcal $m^{-2}$ $yr^{-1}$) in England with large populations of Tipulidae (Macfadyen, 1963, after data from Cragg, 1961). Other grassland data are of the same order as for Spikbole, or lower. Macfadyen (*op. cit.*) calculated the annual respiration to be 7.4 kcal $m^{-2}$ $yr^{-1}$ in a grazed meadow in England, Olechowicz (1976) estimated the respiration of coprophagous Diptera larvae to be 21 kcal $m^{-2}$ during the sheep grazing period in a grazed pasture in Poland, and Hofsvang (1973) calculated the annual respiration of larvae, pupae and adults of *Tipula excisa* to be 5.8 kcal $m^{-2}$ $yr^{-1}$ in a high-altitude tussock field in Norway.

**Feeding habits**

Most soil-inhabiting Nematocera larvae are considered to be saprovorous, although herbivorous, fungivorous and carnivorous forms are also represented within this group. The larvae of Tipulidae are generally classified as saprovores but may also feed on plant roots (Brauns, 1954a). *Bibio* larvae may cause damage to the below-ground parts of various crops (Bollow, 1954), but they are primarily considered to be saprovores (Raw, 1967). The larvae of Cecidomyiidae belong to different feeding categories Some forms

are herbivores, for example gall-inducers, while others are fungivores, carnivores or coprophages (Brauns, 1954a).

In contrast to the predominantly saprovorous Nematocera a significant part of the soil-inhabiting Brachycera-Orthorrhapha ("lower flies") are carnivorous. The larvae of Rhagionidae, Tabanidae, Therevidae, Empididae and Dolichopodidae are predominantly predacious (Brauns, 1954a).

The feeding habits of the larvae belonging to Brachycera-Cyclorrhapha ("higher flies") are more diverse, and especially those of Syrphidae larvae are extremely varied. Some Syrphidae larvae are saprovorous and occur in moist organic matter, mud, or dung. Others occur in rotting wood, while certain forms are pests of, for example, narcissus bulbs (Raw, 1967). Most of the species found at Spikbole (cf. Appendix 2), e.g. *Melanostoma* sp., *Sphaerophoria* spp. and *Syrphus* spp., have larvae that are predators on aphids (cf. Brauns, 1954a). Some Cyclorrhapha species such as *Oscinella frit* L. (Chloropidae) and *Delia* (= *Leptohylemyia*) *coarctata* Fall. are important crop pests and are herbivorous in the larval stage. Many other Cyclorrhapha species, for example *Fannia* species and some other Muscidae larvae are saprovorous and feed on carrion, faeces and/or decaying plant material, but Muscidae also contain predatory forms (Brauns, *op. cit.*). Certain larvae of Calliphoridae are parasitic, among which *Pollenia rudis* Fabr. parasitizes lumbricids of the genus *Allolobophora* (Raw, 1967).

The classification into the main feeding categories according to Fig. 1 was complicated both by incomplete literature data on feeding habits and by taxonomic problems in identifying the larvae. Each taxonomic group was classified as belonging to only one feeding category although several feeding habits could have been recognized within it. Thus, the larvae of Nematocera, Acalyptrata sp., Muscidae sp. and Cyclorrhapha sp. were considered to be saprovores/microbivores, while the larvae of Rhagionidae, Tabanidae, Therevidae, Empididae, Dolichopodidae and Syrphidae were carnivores. The pupae were classified in accordance with the feeding habits of the larvae.

## ARANEAE

### Background

Members of the spider families Gnaphosidae, Clubionidae, Lycosidae, Erigonidae and Linyphiidae are closely associated with the soil environment and are often considered as belonging to the soil fauna. The abundances of spiders have been estimated at about 1–850 specimens $m^{-2}$ in different temperate habitats (Duffey, 1962; Cherrett, 1964; Turnbull, 1973; Delchev & Kajak, 1974). Biomass data are much sparser than abundance data, the estimates usually being of the order 1–150 mg dw $m^{-2}$.

### Methods

The spiders were extracted by Tullgren funnels but, since Tullgren funnel extraction was not used in May, the "summer" and annual means were based on only four "summer" samplings. The spiders were identified, dried at +60°C in a vacuum-drier and

weighed individually to the nearest 0.01 mg. The dry body weights were assumed to be 27 % of the live weights according to Edgar (1971).

The oxygen consumption rates were calculated for each individual spider according to $Q = 127.35 \cdot W^{0.92}$ at +15°C, where $Q$ denotes $mm^3$ $O_2$ $ind^{-1}$ $h^{-1}$ and $W$ denotes g live body weight. This equation is derived from Moulder & Reichle's (1972) equation 13 for lycosids. The rates were corrected to the field temperature using a $Q_{10} = 2$ for temperatures between +15 and +5°C and a $Q_{10} = 3$ below +5°C. The $Q_{10}$ value between +15 and +5°C is similar to that given by Van Hook (1971) for *Pardosa* (*Lycosa*) *rabida* (Walck.) between +15 and +25°C.

## Results

### Species composition

Nineteen species of Araneae were observed in the soil cores from Spikbole (cf. Appendix 2). Only adult spiders were determined to the species level, while juveniles were not identified beyond the genus level. Six spider families were represented in the samples, namely, Gnaphosidae, Clubionidae, Philodromidae, Lycosidae, Erigonidae and Linyphiidae.

### Abundance

Erigonidae, Linyphiidae and Lycosidae were the most abundant spider families with annual mean densities of about 90, 60 and 30 specimens $m^{-2}$, respectively (Table 37). The dominant adults were *Gongylidiellum murcidum* Sim. with 9.8 (*s.e.* = 3.4) $m^{-2}$, *Lepthyphantes holmi* Kronest. with 8.5 (*s.e.* = 6.2) $m^{-2}$ and *Savignya frontata* Bl. with 8.2 (*s.e.* = 2.8) $m^{-2}$. The number of juveniles exceeded that of adults on all sampling occasions. The annual mean number of juveniles was 77 % of the total annual means of 197 (*s.e.* = 38) specimens $m^{-2}$ (Table 37).

### Biomass

The highest biomasses were estimated for *Pardosa fulvipes* (Collett), *Lepthyphantes holmi* and *Allomengea scopigera* (Grube) with 6.5 (*s.e.* = 6.5), 2.3 (*s.e.* = 1.7) and 1.6 (*s.e.* = 1.6) mg dw $m^{-2}$, respectively, when only the identified adults are taken into consideration (Table 38). These estimates are, however, uncertain since they are based on very few individuals. The biomass of Araneae was dominated by the families Lycosidae, Linyphiidae and Erigonidae, which contributed about 18, 11 and 8 mg dw $m^{-2}$, respectively, to the total annual mean biomass of 39 (*s.e.* = 2.6) mg dw $m^{-2}$. The juveniles accounted for 59 % of the total annual mean biomass.

### Respiration

The oxygen consumption rates and annual respiration of Araneae are shown in Table 39. The annual respiration of Lycosidae, Linyphiidae and Erigonidae was estimated at about 0.30, 0.17 and 0.13 kcal $m^{-2}$, respectively. The high respiration of the lycosid *Pardosa fulvipes* of 0.13 (*s.e.* = 0.13) kcal $m^{-2}$ $yr^{-1}$ can be assigned to a single adult obtained in June, and this large lycosid alone contributed 20 % of the total spider respiration of 0.63 (*s.e.* = 0.07) kcal $m^{-2}$ $yr^{-1}$.

Table 37. Abundance (no. $m^{-2}$) of Araneae in 1971–72. The "summer" and annual means are based on only four "summer" samplings. Standard error is given within parentheses below the corresponding mean value.

| | | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|
| Gnaphosidae sp. | juv | 5.3 (5.3) | 0 | 0 | 0 | 1.3 (1.3) | 0 | 0.9 (0.9) |
| *Clubiona* sp. | juv | 0 | 0 | 16.0 (16.0) | 0 | 4.0 (4.0) | 0 | 2.7 (2.7) |
| Clubionidae sp. | juv | 0 | 5.3 (5.3) | 0 | 5.3 (5.3) | 2.7 (1.6) | 7.2 (5.6) | 4.2 (2.2) |
| Philodromidae sp. | juv | 0 | 5.3 (5.3) | 5.3 (5.3) | 0 | 2.7 (1.6) | 0 | 1.8 (1.1) |
| *Pardosa fulvipes* | ad | 5.3 (5.3) | 0 | 0 | 0 | 1.3 (1.3) | 0 | 0.9 (0.9) |
| *Pardosa* sp. | juv | 0 | 0 | 0 | 5.3 (5.3) | 1.3 (1.3) | 0 | 0.9 (0.9) |
| Lycosidae sp. | juv | 5.3 (5.3) | 37.2 (13.9) | 74.5 (27.7) | 26.6 (11.9) | 35.9 (14.5) | 10.3 (5.8) | 27.4 (9.9) |
| *Ceratinella brevipes* | ad | 0 | 0 | 5.3 (5.3) | 0 | 1.3 (1.3) | 0 | 0.9 (0.9) |
| *Dicymbium tibiale* | ad | 0 | 0 | 0 | 0 | 0 | 6.1 (4.7) | 2.1 (1.6) |
| *D. nigrum* | ad | 0 | 5.3 (5.3) | 10.6 (7.1) | 0 | 4.0 (2.6) | 0 | 2.7 (1.7) |
| *Oedothorax retusus* | ad | 0 | 0 | 5.3 (5.3) | 0 | 1.3 (1.3) | 0 | 0.9 (0.9) |
| *Tiso vagans* | ad | 0 | 0 | 0 | 0 | 0 | 3.6 (3.6) | 1.2 (1.2) |
| *Gongylidiellum murcidum* | ad | 5.3 (5.3) | 16.0 (11.4) | 5.3 (5.3) | 5.3 (5.3) | 8.0 (2.7) | 13.3 (8.5) | 9.8 (3.4) |
| *Latithorax faustus* | ad | 0 | 0 | 5.3 (5.3) | 0 | 1.3 (1.3) | 0 | 0.9 (0.9) |
| *Micrargus herbigradus* | ad | 0 | 5.3 (5.3) | 0 | 0 | 1.3 (1.3) | 0 | 0.9 (0.9) |
| *Erigonella hiemalis* | ad | 0 | 0 | 0 | 0 | 0 | 6.1 (4.7) | 2.1 (1.6) |
| *Savignya frontata* | ad | 0 | 10.6 (7.1) | 10.6 (7.1) | 16.0 (16.0) | 9.3 (3.4) | 6.1 (4.7) | 8.2 (2.8) |
| Erigonidae sp. | juv | 10.6 (10.6) | 111.7 (20.2) | 79.8 (35.7) | 63.8 (22.2) | 66.5 (21.2) | 51.4 (17.5) | 61.5 (15.3) |
| *Centromerita bicolor* | ad | 0 | 0 | 0 | 5.3 (5.3) | 1.3 (1.3) | 0 | 0.9 (0.9) |
| *Bathyphantes gracilis* | ad | 0 | 0 | 5.3 (5.3) | 0 | 1.3 (1.3) | 4.3 (4.3) | 2.3 (1.7) |
| *Lepthyphantes angulatus* | ad | 0 | 0 | 5.3 (5.3) | 0 | 1.3 (1.3) | 0 | 0.9 (0.9) |
| *L. holmi* | ad | 5.3 (5.3) | 0 | 37.2 (21.1) | 0 | 10.6 (9.0) | 4.3 (4.3) | 8.5 (6.2) |
| *L.* sp. | juv | 0 | 0 | 5.3 (5.3) | 5.3 (5.3) | 2.7 (1.6) | 0 | 1.8 (1.1) |
| *Allomengea scopigera* | ad | 0 | 5.3 (5.3) | 0 | 0 | 1.3 (1.3) | 0 | 0.9 (0.9) |
| Linyphiidae sp. | juv | 47.9 (20.2) | 106.4 (83.6) | 26.6 (18.2) | 53.2 (37.2) | 58.5 (17.0) | 24.9 (12.8) | 47.3 (12.1) |
| not determined | juv | 0 | 0 | 0 | 0 | 0 | 9.7 (5.2) | 3.2 (1.7) |
| juveniles, total | | 69 (23) | 266 (78) | 207 (75) | 154 (52) | 174 (42) | 98 (29) | 149 (30) |
| adults, total | | 16 (12) | 43 (21) | 90 (27) | 32 (17) | 45 (16) | 44 (12) | 45 (12) |
| Araneae, total | | 85 (22) | 309 (81) | 298 (97) | 186 (57) | 219 (53) | 151 (37) | 197 (38) |

Table 38. Biomass (mg dry weight $m^{-2}$) of Araneae in 1971–72. The "summer" and annual means are based on only four "summer" samplings. Standard error is given within parentheses below the corresponding mean value.

| | | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|
| Gnaphosidae sp. | juv | 2.0 (2.0) | 0 | 0 | 0 | 0.5 (0.5) | 0 | 0.3 (0.3) |
| *Clubiona* sp. | juv | 0 | 0 | 2.6 (2.6) | 0 | 0.6 (0.6) | 0 | 0.4 (0.4) |
| Clubionidae sp. | juv | 0 | 0.5 (0.5) | 0 | 0.5 (0.5) | 0.3 (0.2) | 2.3 (2.1) | 0.9 (0.7) |
| Philodromidae sp. | juv | 0 | 0.6 (0.6) | 0.8 (0.8) | 0 | 0.4 (0.3) | 0 | 0.2 (0.2) |
| *Pardosa fulvipes* | ad | 39.2 (39.2) | 0 | 0 | 0 | 9.8 (9.8) | 0 | 6.5 (6.5) |
| *Pardosa* sp. | juv | 0 | 0 | 0 | 7.5 (7.5) | 1.9 (1.9) | 0 | 1.2 (1.2) |
| Lycosidae sp. | juv | 3.7 (3.7) | 16.0 (9.9) | 24.5 (10.0) | 9.6 (4.2) | 13.5 (4.5) | 4.4 (2.8) | 10.5 (3.2) |
| *Ceratinella brevipes* | ad | 0 | 0 | 0.7 (0.7) | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *Dicymbium tibiale* | ad | 0 | 0 | 0 | 0 | 0 | 1.2 (0.9) | 0.4 (0.3) |
| *D. nigrum* | ad | 0 | 1.3 (1.3) | 2.6 (1.8) | 0 | 1.0 (0.7) | 0 | 0.7 (0.5) |
| *Oedothorax retusus* | ad | 0 | 0 | 0.7 (0.7) | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *Tiso vagans* | ad | 0 | 0 | 0 | 0 | 0 | 0.6 (0.6) | 0.2 (0.2) |
| *Gongylidiellum murcidum* | ad | 0.7 (0.7) | 1.5 (1.2) | 0.4 (0.4) | 0.7 (0.7) | 0.8 (0.3) | 1.5 (1.0) | 1.1 (0.4) |
| *Latithorax faustus* | ad | 0 | 0 | 0.4 (0.4) | 0 | 0.1 (0.1) | 0 | 0.1 (0.1) |
| *Micrargus herbigradus* | ad | 0 | 1.4 (1.4) | 0 | 0 | 0.4 (0.4) | 0 | 0.3 (0.3) |
| *Erigonella hiemalis* | ad | 0 | 0 | 0 | 0 | 0 | 0.8 (0.6) | 0.3 (0.2) |
| *Savignya frontata* | ad | 0 | 1.2 (0.9) | 1.8 (1.2) | 2.9 (2.9) | 1.5 (0.7) | 0.7 (0.6) | 1.2 (0.5) |
| Erigonidae sp. | juv | 0.1 (0.1) | 7.6 (2.3) | 3.8 (1.5) | 3.9 (1.7) | 3.9 (1.6) | 2.7 (1.1) | 3.5 (1.1) |
| *Centromerita bicolor* | ad | 0 | 0 | 0 | 3.2 (3.2) | 0.8 (0.8) | 0 | 0.5 (0.5) |
| *Bathyphantes gracilis* | ad | 0 | 0 | 1.9 (1.9) | 0 | 0.5 (0.5) | 0.6 (0.6) | 0.5 (0.4) |
| *Lepthyphantes angulatus* | ad | 0 | 0 | 1.0 (1.0) | 0 | 0.2 (0.2) | 0 | 0.2 (0.2) |
| *L. holmi* | ad | 2.1 (2.1) | 0 | 10.6 (6.3) | 0 | 3.2 (2.6) | 0.6 (0.6) | 2.3 (1.7) |
| *L.* sp. | juv | 0 | 0 | 0.4 (0.4) | 1.6 (1.6) | 0.5 (0.4) | 0 | 0.3 (0.3) |
| *Allomengea scopigera* | ad | 0 | 9.4 (9.4) | 0 | 0 | 2.3 (2.3) | 0 | 1.6 (1.6) |
| Linyphiidae sp. | juv | 2.7 (1.5) | 3.5 (1.8) | 2.3 (1.9) | 22.7 (21.2) | 7.8 (5.0) | 1.9 (1.1) | 5.8 (3.4) |
| not determined | juv | 0 | 0 | 0 | 0 | 0 | 0.2 (0.1) | 0.1 (0.1) |
| juveniles, total | | 8.5 (4.5) | 28 (9.6) | 34 (13) | 46 (24) | 29 (7.8) | 11 (4.6) | 23 (5.5) |
| adults, total | | 42 (42) | 15 (9.5) | 20 (6.8) | 6.8 (4.1) | 21 (7.6) | 5.9 (1.7) | 16 (5.1) |
| Araneae, total | | 50 (41) | 43 (19) | 55 (17) | 53 (24) | 50 (2.5) | 17 (5.7) | 39 (2.6) |

Table 39. Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) and annual respiration (kcal $m^{-2}$) of Araneae in 1971–72. The "summer" and annual means are based on only four "summer" samplings. Standard error is given within parentheses below the corresponding mean value. + denotes a value less than 0.0005.

| | | Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) | | | | | | | Annual respiration (kcal $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|
| | | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual | |
| Gnaphosidae sp. | juv | 0.028 (0.028) | 0 | 0 | 0 | 0.007 (0.007) | 0 | 0.005 (0.005) | 0.008 (0.008) |
| *Clubiona* sp. | juv | 0 | 0 | 0.026 (0.026) | 0 | 0.006 (0.006) | 0 | 0.004 (0.004) | 0.008 (0.008) |
| Clubionidae sp. | juv | 0 | 0.007 (0.007) | 0 | 0.004 (0.004) | 0.003 (0.002) | 0.011 (0.010) | 0.006 (0.004) | 0.010 (0.007) |
| Philodromidae sp. | juv | 0 | 0.008 (0.008) | 0.008 (0.008) | 0 | 0.004 (0.003) | 0 | 0.003 (0.002) | 0.005 (0.003) |
| *Pardosa fulvipes* | ad | 0.427 (0.427) | 0 | 0 | 0 | 0.107 (0.107) | 0 | 0.071 (0.071) | 0.125 (0.125) |
| *Pardosa* sp. | juv | 0 | 0 | 0 | 0.043 (0.043) | 0.011 (0.011) | 0 | 0.007 (0.007) | 0.013 (0.013) |
| Lycosidae sp. | juv | 0.049 (0.049) | 0.174 (0.101) | 0.235 (0.094) | 0.062 (0.028) | 0.130 (0.045) | 0.022 (0.014) | 0.094 (0.031) | 0.165 (0.054) |
| *Ceratinella brevipes* | ad | 0 | 0 | 0.008 (0.008) | 0 | 0.002 (0.002) | 0 | 0.001 (0.001) | 0.002 (0.002) |
| *Dicymbium tibiale* | ad | 0 | 0 | 0 | 0 | 0 | 0.006 (0.005) | 0.002 (0.002) | 0.004 (0.003) |
| *D. nigrum* | ad | 0 | 0.016 (0.016) | 0.026 (0.018) | 0 | 0.010 (0.007) | 0 | 0.007 (0.005) | 0.012 (0.008) |
| *Oedothorax retusus* | ad | 0 | 0 | 0.007 (0.007) | 0 | 0.002 (0.002) | 0 | 0.001 (0.001) | 0.002 (0.002) |
| *Tiso vagans* | ad | 0 | 0 | 0 | 0 | 0 | 0.003 (0.003) | 0.001 (0.001) | 0.002 (0.002) |
| *Gongylidiellum murcidum* | ad | 0.011 (0.011) | 0.020 (0.015) | 0.005 (0.005) | 0.005 (0.005) | 0.010 (0.004) | 0.008 (0.006) | 0.010 (0.004) | 0.017 (0.006) |
| *Latithorax faustus* | ad | 0 | 0 | 0.005 (0.005) | 0 | 0.001 (0.001) | 0 | 0.001 (0.001) | 0.001 (0.001) |
| *Micrargus herbigradus* | ad | 0 | 0.017 (0.017) | 0 | 0 | 0.004 (0.004) | 0 | 0.003 (0.003) | 0.005 (0.005) |
| *Erigonella hiemalis* | ad | 0 | 0 | 0 | 0 | 0 | 0.005 (0.004) | 0.002 (0.002) | 0.003 (0.003) |
| *Savignya frontata* | ad | 0 | 0.015 (0.011) | 0.018 (0.013) | 0.020 (0.020) | 0.013 (0.005) | 0.004 (0.004) | 0.010 (0.004) | 0.018 (0.006) |
| Erigonidae sp. | juv | 0.002 (0.002) | 0.098 (0.029) | 0.043 (0.018) | 0.028 (0.012) | 0.043 (0.021) | 0.015 (0.006) | 0.034 (0.014) | 0.059 (0.025) |
| *Centromerita bicolor* | ad | 0 | 0 | 0 | 0.020 (0.020) | 0.005 (0.005) | 0 | 0.003 (0.003) | 0.006 (0.006) |
| *Bathyphantes gracilis* | ad | 0 | 0 | 0.019 (0.019) | 0 | 0.005 (0.005) | 0.003 (0.003) | 0.004 (0.004) | 0.008 (0.006) |
| *Lepthyphantes angulatus* | ad | 0 | 0 | 0.010 (0.010) | 0 | 0.002 (0.002) | 0 | 0.002 (0.002) | 0.003 (0.003) |
| *L. holmi* | ad | 0.029 (0.029) | 0 | 0.103 (0.061) | 0 | 0.033 (0.025) | 0.003 (0.003) | 0.023 (0.017) | 0.041 (0.029) |
| *L.* sp. | juv | 0 | 0 | 0.005 (0.005) | 0.011 (0.011) | 0.004 (0.003) | 0 | 0.003 (0.002) | 0.005 (0.004) |
| *Allomengea scopigera* | ad | 0 | 0.096 (0.096) | 0 | 0 | 0.024 (0.024) | 0 | 0.016 (0.016) | 0.028 (0.028) |
| Linyphiidae sp. | juv | 0.042 (0.023) | 0.047 (0.024) | 0.025 (0.020) | 0.130 (0.120) | 0.061 (0.024) | 0.011 (0.007) | 0.044 (0.016) | 0.078 (0.028) |
| not determined | juv | 0 | 0 | 0 | 0 | 0 | 0.001 (0.001) | + | + |
| juveniles, total | | 0.121 (0.060) | 0.335 (0.100) | 0.342 (0.120) | 0.278 (0.137) | 0.269 (0.052) | 0.060 (0.024) | 0.199 (0.035) | 0.350 (0.062) |
| adults, total | | 0.467 (0.455) | 0.164 (0.098) | 0.200 (0.066) | 0.045 (0.027) | 0.219 (0.089) | 0.033 (0.009) | 0.157 (0.060) | 0.276 (0.105) |
| Araneae, total | | 0.588 (0.445) | 0.498 (0.190) | 0.542 (0.161) | 0.322 (0.133) | 0.488 (0.058) | 0.093 (0.030) | 0.356 (0.040) | 0.625 (0.070) |

## Discussion

### Abundance

The Tullgren funnel extraction, or modifications of this method, seems to give reliable estimates of the numbers of Araneae (cf. Turnbull, 1973). It is, for example, far more efficient than hand sorting (Huhta, 1972). The sample unit of only 188 $cm^2$ surface area and the small sample size ($n$ = 10) at the "summer" samplings were probably too small for obtaining accurate abundance estimates of the larger and more sparsely distributed spiders such as Lycosidae (cf. van der Drift, 1951; Duffey, 1962). The estimates of these large spiders must therefore be considered as uncertain, which is also indicated by the large standard errors. A possible source of error is that mobile spiders might have escaped from the selected area before the sampler was forced into the soil.

The total numbers of Araneae at Spikbole ranging from 85 to 309 individuals $m^{-2}$ and the annual mean of about 200 $m^{-2}$ are similar to many estimates obtained in other grasslands. Annual means ranging from 140 to 623 $m^{-2}$ have been reported by Bristowe (1939), Duffey (1962) and Cherrett (1964) in unmanaged English grasslands. Summer mean abundances of the order 50 $m^{-2}$ have been obtained in alpine meadow sites in Norway (Naess *et al.*, 1975; Østbye *et al.*, 1975). The spider densities are generally higher in unmanaged grasslands than in managed ones (Delchev & Kajak, 1974). Estimates ranging from 14 to 180 $m^{-2}$ have been reported for utilized meadows and pastures by Salt *et al.* (1948), Cherrett (*op. cit.*) and Delchev & Kajak (*op. cit.*), among others.

### Biomass

The annual mean biomass of about 40 mg dw $m^{-2}$ at Spikbole is in agreement with the annual means reported by Cherrett (1964) in unmanaged grasslands in a high altitude area in England, where he found 47 and 39 mg dw $m^{-2}$ in *Festuca/Nardus* and *Juncus squarrosus* sites, respectively. He also obtained an annual mean of 16 mg dw $m^{-2}$ in a *Calluna/Eriophorum* locality, but only 3–4 mg dw $m^{-2}$ in a grazed limestone grassland in the same area. Delchev & Kajak (1974) reported average values of 40–56 mg dw $m^{-2}$ in a Bulgarian pasture and 2.3–4.2 mg dw $m^{-2}$ in a Polish pasture during the grazing season for sheep. Naess *et al.* (1975) recorded summer means of 3.7–4.5 mg dw $m^{-2}$ in a dry alpine meadow and 5.5–11.3 mg dw $m^{-2}$ in a wet alpine meadow in Norway. A much higher value, 6 g fw $m^{-2}$, was reported by Macfadyen (1963) for a grazed meadow in England.

### Respiration

The relationship between oxygen consumption rate and body size of spiders has been studied by several authors, for example Itô (1964), Miyashita (1969), Anderson (1970), Van Hook (1971), Moulder & Reichle (1972), Humphreys (1975) and Steigen (1975b). The equation at +15°C given by Moulder & Reichle (*op. cit.*) and used in this study was, therefore, only one of many alternatives. The choice of equation in calculating oxygen consumption rates was difficult, since the equations differed considerably. However, when the oxygen consumption rates of the spiders at Spikbole were calculated according to either Humphreys (*op. cit.*) or Steigen (1975a, b) the results were quite comparable with those obtained according to the present method.

Several factors such as locomotion, moulting, feeding and starvation affect the respiratory metabolism in spiders as well as in other invertebrates. Miyashita (1969) found, for example, that the respiratory energy loss for the lycosid *Pardosa* (*Lycosa*) *T-insignita* (Bös. & Str.) was 3–6 times higher during locomotory activity than during rest. Long periods of activity may, thus, enhance the total respiration considerably over the standard respiration level. This was also indicated by the results reported by Hagstrum (1970), who observed a two-fold higher weight loss rate in the field than in the laboratory between two feedings of the lycosid *Tarentula kochi* Keyserling, a fact that he interpreted as induced by greater activity and, consequently, increased respiration in the field. However, enhanced respiration caused by locomotion is probably more pronounced for hunting spiders like Lycosidae than for web-building spiders like Linyphiidae and Erigonidae, which have much shorter periods of locomotory activity.

Other factors affecting the respiratory rate are moulting and feeding, which according to Hagstrum (*op. cit.*) increased the respiration 4.3-fold and 3-fold, respectively, for *T. kochi*. Starvation, on the other hand, reduces the respiratory metabolism. Collatz & Mommsen (1975) found a small but obvious reduction in respiratory rate after 7 days of starvation for *Tegenaria atrica* C.L.K., and after 50 days of starvation the respiration was only 17 % of the normal. All these factors are very difficult to evaluate when calculating the field respiration, and since they also affect the respiration in opposite directions, they have not been taken into consideration in the present study.

The annual respiration of Araneae of 0.63 (*s.e.* = 0.07) kcal $m^{-2}$ $yr^{-1}$ at Spikbole is similar to many other estimates of spider respiration. Moulder & Reichle (1972) calculated, for example, the spider respiration to be 1.23 kcal $m^{-2}$ $yr^{-1}$ in a *Liriodendron* forest floor in Tennessee, Heal *et al.* (1975) found an annual respiration of 0.17 g $m^{-2}$ or about 0.85 kcal $m^{-2}$ in an upland blanket bog in England, and Huhta & Koskenniemi (1975) obtained respiration figures of 0.2–0.8 kcal $m^{-2}$ $yr^{-1}$ for the spider fauna in three spruce forest soils in Finland. Higher respiration estimates have been reported by Macfadyen (1963), who found an annual respiration of 34.3 kcal $m^{-2}$ in a grazed meadow in England. Annual respiration figures concerning individual species or genera have been reported by some authors, of whom Van Hook (1971) calculated the annual respiration of *Pardosa* (*Lycosa*) spp. to be 3.84 kcal $m^{-2}$ in a *Festuca/Andropogon* grassland in Tennessee, and Steigen (1975b) calculated the annual respiration to be 0.067 kcal $m^{-2}$ for *Pardosa palustris* (L.) in a dry alpine meadow in Norway.

**Feeding habits**

Extensive records indicate that spiders are unspecific predators of other invertebrates (e.g. Turnbull, 1973). Different kinds of spiders use different strategies in capturing the prey, and web-building spiders such as Linyphiidae and Erigonidae will therefore feed on other prey animals than hunting spiders such as Gnaphosidae, Clubionidae, Philodromidae and Lycosidae. All Araneae can be classified as carnivores, and in this study the spiders obtained have been considered as below-ground carnivores according to Fig. 1.

## Background

Acari is often the most abundant soil arthropod group in temperate localities, and there are only few habitats where the number of Collembola exceeds that of Acari (Lebrun, 1971). The mean abundances of Acari are often estimated at 10 000–300 000 $m^{-2}$ (cf. Curry, 1969), but higher densities than 300 000 $m^{-2}$ are not infrequently recorded in various mor soils (e.g. Forsslund, 1943; Murphy, 1953; Wallwork, 1959; Axelsson *et al.*, 1973b; Vtorov & Martynova, 1974; Huhta & Koskenniemi, 1975; Persson, 1975). The biomasses are often estimated at 50–1500 mg dw $m^{-2}$. In general, litter- and soil-inhabiting Acari belong to one of the four orders (or sub-orders) Mesostigmata, Prostigmata, Astigmata and Cryptostigmata. Cryptostigmata (Oribatei) seems to be the dominant acarine group in many localities, but Prostigmata is found to have higher densities in some soils.

## Methods

The sample units and extraction methods used for Acari were identical with those used for Collembola. The mites were identified to the species level if possible. The determination of the Mesostigmata groups Gamasina and Uropodina followed Karg (1971) and Evans (1957, 1972), respectively. Prostigmata was determined to the family level according to Krantz (1971), while the further identification was made by the works of Vitzthum (1929), Thor (1931, 1933), Thor & Willmann (1941), Krczal (1959), Karafiat (1959) and Schaarschmidt (1959). Species belonging to Astigmata were determined according to Scheucher (1957) and Türk & Türk (1957). Adult Cryptostigmata were mainly classified to the genus level according to Balogh (1963, 1972), while the identification keys by Sellnick (1929, 1960), Willmann (1931) and Niedbala (1974), among others, were used for species determination. The classification of Acari into Mesostigmata, Prostigmata, Astigmata and Cryptostigmata suggested by Evans *et al.* (1961) was used in the text and tables, since this classification is commonly used by ecologists. The classification in Appendix 2 into the orders Parasitiformes and Acariformes (Zachvatkin, 1952) is more often used by taxonomists.

The identified Acari were separated into adults and juveniles, except for Prostigmata and Astigmata, and different mean weights were calculated for each category (Tables 40 and 41). The largest Mesostigmata, Prostigmata and Cryptostigmata were vacuum-dried at +60°C and weighed to the nearest 0.01 mg, but the mean weights of the majority of Acari had to be calculated from regression equations based on weight and width determinations. Therefore, the body lengths and widths were measured on a number of specimens (about 20 per species for abundantly occurring species), and the corresponding mean weights are given in Tables 40 and 41.

Lebrun (1971) developed a multiple regression equation which expressed the relationship between the weight and the length and width of about 20 oribatid species. This equation was:

$$\log W = 1.53 \log L + 1.53 \log l - 6.67$$

where $W$ denotes the live body weight in $\mu$g, $L$ the body length in $\mu$m and $l$ the body width in $\mu$m at the widest point. Lebrun (*op. cit.*) found that weights calculated according to this equation sometimes deviated strongly from the actual weights, but it was possible to obtain more accurate estimates by classifying different oribatid species to certain morphological types. The equations for these types were:

"Achipteriformes": $\log W = 2.09 \log L + 0.93 \log l - 6.67$

"Carabodiformes": $\log W = 1.62 \log L + 1.40 \log l - 6.56$

"Nothroiformes": $\log W = 2.09 \log L + 0.84 \log l - 6.44$

The latter three equations were used for calculating the weights of most adult oribatids at Spikbole, while the first equation was used for those adult oribatids which could not be assigned to any of the three morphological types. The juvenile stages were usually not separated from each other and, therefore, the same mean weight of the juveniles of a species had to be used independent of the season. The mean weights of juvenile Cryptostigmata were assumed to be one-fourth of those of the corresponding adults, i.e. approximately equivalent to the deutonymphal weight (cf. Luxton, 1975).

The mean weights of the species belonging to Astigmata were calculated from the first of the equations above. The mean weights of the Prostigmata species were based on Edwards' (1967) equation for Trombidiformes, i.e. $\sqrt[3]{W} = 0.00387 \cdot L$ when given in a form equivalent to those above. Edwards' (*op. cit.*) equations for Parasitidae and Uropodina predicted weights that were much lower than those measured on an electrobalance for the corresponding species from Spikbole. More satisfactory estimates were obtained when Lebrun's (1971) equation for "Nothroiformes" was used with a correction factor of 0.85. Thus, the equation $W = 0.85\ (L^{2.09} \cdot l^{0.84} \cdot 10^{-6.44})$ (cf. Table 40) was used for all smaller mesostigmatids at Spikbole. The dry weight/live weight ratio was assumed to be 0.40 for all Acari, which is in the region of the ratios given by Block (1966a), Edwards (1967) and Luxton (1975).

The relationship between oxygen consumption rate per individual ($Q$) and live body weight ($W$) is generally given in the form $Q = a \cdot W^b$ (cf. General methods, p. 36). Since the Acari species were usually not separated into more than the juvenile and adult stages, the mean live body weight of each stage (cf. Tables 40 and 41) was used as a substitute for $W$ in the equation. The oxygen consumption rates at +10°C of Gamasina were calculated from the equation given by Wood & Lawton (1973) for "adult and juvenile Gamasina excluding *Epicrius*", and the rates of Uropodina were obtained from the equation for "adult Uropodina" (Wood & Lawton, *op. cit.*) (cf. Table 42). Wood & Lawton have also presented an equation for adult Prostigmata based on 13 individual measurements, $Q = 853.1 \cdot W^{1.033}$, where $Q$ denotes $mm^3\ O_2\ ind^{-1}\ h^{-1}$ at +10°C and $W$ denotes the live body weight in g. When the equation for Prostigmata is used for calculating oxygen consumption rates of small Prostigmata weighing less than 1 $\mu$g live body weight, which is outside the validity range of the regression, the unusually high value of the exponent $b$ causes the rates to become lower for Prostigmata than for Cryptostigmata of the same size. This seems unlikely, since prostigmatid mites are considered to be extremely active in comparison with Cryptostigmata and Uropodina (Wood & Lawton, *op. cit.*), and since the equation was based on very few determinations, the equation for Gamasina was also used for Prostigmata.

Table 40. Mean body lengths, widths and weights for different Mesostigmata species at Spikbole. Dry weight content is assumed to be 40 % of live weight.

$N_2$ = deutonymph
$W$ = mean live body weight in $\mu$g
$L$ = idiosoma mean length in $\mu$m
$l$ = idiosoma mean width in $\mu$m at the widest point

| Species | Stage | $L$ ($\mu$m) | $l$ ($\mu$m) | Live wt ($\mu$g) | Dry wt ($\mu$g) | Weight calculation (see below) |
|---|---|---|---|---|---|---|
| Gamasina | | | | | | |
| *Pachylaelaps* cf. *laeuchlii* | ad | 830 | 600 | 84 | 34 | (2) |
| *Hypoaspis nolli* | ad | 500 | 300 | 16 | 6.5 | (2) |
| *H.* sp. | ad | 500 | 300 | 16 | 6.5 | (2) |
| *H.* sp. | juv | | | 5 | 2.0 | (3) |
| *Amblyseius obtusus/ okanagensis* | ad | 420 | 275 | 10.5 | 4.2 | (2) |
| *Lasioseius berlesei* | ad | 530 | 320 | 19 | 7.75 | (2) |
| *L. berlesei* | juv | | | 6.5 | 2.6 | (3) |
| *Cheiroseius borealis* | $N_2$ | 500 | 300 | 16 | 6.5 | (2) |
| *Arctoseius cetratus* | ad | 360 | 180 | 5.3 | 2.1 | (2) |
| *A. insularis* | ad | 340 | 200 | 5.2 | 2.1 | (2) |
| *A. insularis* | juv | | | 1.75 | 0.7 | (3) |
| *Mixozercon sellnicki* | ad | 330 | 230 | 5.5 | 2.2 | (2) |
| *M. sellnicki* | juv | | | 1.75 | 0.7 | (3) |
| *Rhodacarellus silesiacus* | ad | 300 | 115 | 2.5 | 1.0 | (2) |
| *Dendrolaelaps* sp. | ad | 340 | 200 | 5.2 | 2.1 | (2) |
| *Cyrtolaelaps mucronatus* | $N_2$ | 780 | 480 | 61 | 24 | (2) |
| *Holoparasitus excipuliger* | ad | 660 | 440 | 62.5 | 25 | (1) |
| *H. excipuliger* | juv | | | 20 | 8 | (3) |
| *Pergamasus brevicornis* | ad | 1200 | 760 | 225 | 90 | (1) |
| *P. septentrionalis* | ad | 1350 | 780 | 300 | 120 | (1) |
| *P. brevicornis/septentrionalis* | $N_2$ | 1000 | 700 | 138 | 55 | (1) |
| *P. misellus* | ad | 540 | 280 | 18 | 7.2 | (2) |
| *P. lapponicus* coll. | ad | 780 | 400 | 50 | 20 | (1) |
| *P.* sp. | juv | 500 | 275 | 15 | 6.0 | (2) |
| *Veigaia kochi* | ad | 1350 | 760 | 225 | 90 | (1) |
| *V. nemorensis* | ad | 700 | 400 | 42.5 | 17 | (1) |
| *V. nemorensis* | juv | | | 15 | 6.0 | (3) |
| *V. cerva* | ad | 860 | 450 | 75 | 30 | (1) |
| *V. cerva* | juv | | | 25 | 10 | (3) |
| Gamasina sp. | juv | | | 5 | 2 | (3) |
| Uropodina | | | | | | |
| *Dinychus* sp. | ad | 820 | 580 | 75 | 30 | (1) |
| *D.* sp. | juv | | | 20 | 8 | (3) |
| Uropodina sp. | ad | 700 | 500 | 60 | 24 | (1) |

(1) = direct weighing
(2) = calculated from the equation $W = 0.85\ (L^{2.09} \cdot l^{0.84} \cdot 10^{-6.44})$
(3) = calculated as (2) but after adjustment for the relative abundance of different juvenile stages

Table 41. Mean body lengths, widths and weights for Prostigmata, Astigmata and Cryptostigmata at Spikbole. Dry weight content is assumed to be 40 % of live weight.

$W$ = mean live body weight in $\mu$g
$L$ = mean body length in $\mu$m
$l$ = mean body width in $\mu$m at the widest point

| Species | Stage | $L$ ($\mu$m) | $l$ ($\mu$m) | Live wt ($\mu$g) | Dry wt ($\mu$g) | Weight calculation (see below) |
|---|---|---|---|---|---|---|
| **Prostigmata** | | | | | | |
| Pyemotidae | juv+ad | 190 | | 0.40 | 0.16 | (6) |
| Scutacaridae | juv+ad | 190 | | 0.40 | 0.16 | (6) |
| Tarsonemidae | juv+ad | 190 | | 0.40 | 0.16 | (6) |
| Eriophyidae | juv+ad | 240 | | 0.80 | 0.32 | (6) |
| Anystidae | ad | 1050 | | 225 | 90 | (1) |
| Other Prostigmata | juv+ad | 240 | | 0.80 | 0.32 | (6) |
| **Astigmata** | | | | | | |
| *Histiostoma* cf. *feroniarum* | juv+ad | 240 | 105 | 1.16 | 0.46 | (2) |
| *Schwiebea cavernicola* | juv+ad | 270 | 125 | 1.80 | 0.72 | (2) |
| Astigmata sp. | juv | 240 | 105 | 1.16 | 0.46 | (2) |
| **Cryptostigmata** | | | | | | |
| *Steganacarus striculus* | ad | | | 25 | 10 | (1) |
| *Hypochthonius rufulus* | ad | | | 25 | 10 | (8) |
| Brachychthoniidae spp. | ad | 210 | 110 | 1.0 | 0.40 | (2) |
| B. spp. | juv | | | 0.25 | 0.10 | (7) |
| *Platynothrus peltifer* | ad | 750 | 380 | 54 | 22 | (5) |
| *P. peltifer* | juv | | | 13.75 | 5.5 | (7) |
| *Damaeus clavipes* | ad | 1080 | 720 | 220 | 88 | (2) |
| *D. verticillipes* | ad | 860 | 600 | 118 | 47 | (2) |
| *D. verticillipes* | juv | | | 30 | 11.75 | (7) |
| *Carabodes areolatus* | ad | 470 | 280 | 20 | 8.0 | (1) |
| *Tectocepheus sarekensis* | ad | 340 | 205 | 6.0 | 2.4 | (4) |
| *T. sarekensis* | juv | | | 1.5 | 0.6 | (7) |
| *Oppia minus* | ad | 210 | 100 | 0.88 | 0.35 | (2) |
| *O. nova* | ad | 270 | 150 | 2.4 | 0.96 | (2) |
| *O. minus/nova* (pooled) | ad | | | 1.5 | 0.6 | (2) |
| *O. minus/nova* (pooled) | juv | | | 0.375 | 0.15 | (7) |
| *Suctobelba subtrigona* | ad | 280 | 150 | 2.5 | 1.0 | (3) |
| *Oribatula tibialis* | ad | 450 | 290 | 15 | 6.0 | (3) |
| *Hemileius initialis* | ad | 520 | 360 | 24 | 9.7 | (3) |
| *Scheloribates laevigatus* | ad | 620 | 410 | 42.5 | 17 | (1) |
| *Chamobates cuspidatus* | ad | 390 | 290 | 10.8 | 4.3 | (3) |
| *Trichoribates trimaculatus* | ad | 760 | 560 | 90 | 36 | (1) |
| *T. trimaculatus* | juv | | | 22.5 | 9.0 | (7) |
| *Neoribates aurantiacus* | ad | 490 | 320 | 19 | 7.7 | (3) |
| Cryptostigmata sp. | juv | 280 | 150 | 2.5 | 1.0 | (2) |

(1) = direct weighing
(2) = calculated from the equation $W = L^{1.53} \cdot l^{1.53} \cdot 10^{-6.67}$ (Lebrun, 1971)
(3) = calculated from the equation $W = L^{2.09} \cdot l^{0.93} \cdot 10^{-6.67}$ (Lebrun, 1971)
(4) = calculated from the equation $W = L^{1.62} \cdot l^{1.40} \cdot 10^{-6.56}$ (Lebrun, 1971)
(5) = calculated from the equation $W = L^{2.09} \cdot l^{0.84} \cdot 10^{-6.44}$ (Lebrun, 1971)
(6) = calculated from the equation $W = (0.00387 \cdot L)^3$ (Edwards, 1967)
(7) = calculated as one-fourth of the adult weight
(8) = live weight given by Luxton (1975)

Table 42. The relationship between live body weight ($W$) and oxygen consumption rate per individual ($Q$) of different Acari groups at +10°C. The relationship is of the form $Q = a \cdot W^b$, where $Q$ is given in $mm^3\ O_2\ ind^{-1}\ h^{-1}$ and $W$ in g.

| | $a$ | $b$ | Reference |
|---|---|---|---|
| Mesostigmata | | | |
| Gamasina | 102.33 | 0.869 | Wood & Lawton (1973) |
| Uropodina | 5.035 | 0.671 | " |
| Prostigmata | 102.33 | 0.869 | see text |
| Astigmata | 102.33 | 0.869 | " |
| Cryptostigmata | | | |
| Ptyctima | 3.464 | 0.6917 | Luxton (1975) |
| Aptyctima | 7.212 | 0.6920 | " |

Data on the oxygen consumption rates of Astigmata are fairly sparse. The rates of *Tyroglyphus linteri* at +25°C (one determination), *Rhizoglyphus echinopus* (F. & R.) at +20°C (one determination) and *Caloglyphus berlesei* (Mich.) at +25°C (determinations of all developmental stages) have been reported by Engelmann (1961), Byzova (1973) after recalculation from Chernova *et al.* (1971) and Stepien & Rodrigues (1972), respectively. The rates deviated relatively little from the equation given for Gamasina (cf. Table 42), when the rates were corrected to a temperature of +10°C assuming a $Q_{10} = 3$, and therefore this equation could also be used for Astigmata.

Berthet (1964, 1967), Wood & Lawton (1973) and Luxton (1975) have all presented regression equations for adult Cryptostigmata. The equation for "total oribatids except macrophytophages" given by Luxton (*op. cit.*) predicts lower rates for oribatids smaller than 100 µg at +10°C than the corresponding equation given by Wood & Lawton (*op. cit.*) while it predicts higher rates than Berthet's (1967) equation for Oribatei at +10°C. In the present investigation Luxton's equations for "total oribatids except macrophytophages" and "macrophytophages" (cf. Table 6 in Luxton, *op. cit.*) were used for calculating the oxygen consumption rates at +10°C for Aptyctima (most Cryptostigmata) and Ptyctima (only *Steganacarus* at Spikbole), respectively. These relations are given in a modified form in Table 42. The relations were used both for adults and juveniles.

Luxton (1975) determined the oxygen consumption rates at different temperatures between +5 and +20°C. According to his temperature correction factor the $Q_{10}$ was about 3 between +5 and +15°C for "total oribatids except macrophytophages". Therefore, $Q_{10} = 3$ was used in calculating oxygen consumption rates of Aptyctima at temperatures down to +5°C assuming an exponential relationship. Below +5°C a $Q_{10} = 4$ was used in accordance with Berthet (1964, 1967). The oxygen consumption rates of Ptyctima were corrected to the field temperature by using $Q_{10} = 3.2$ down to +5°C (Luxton, *op. cit.*) and $Q_{10} = 4$ for lower temperatures (Berthet, 1967). Data on temperature dependence of oxygen consumption rates of other Acari were not found in the literature, and $Q_{10} = 3$ was used at all temperatures for Gamasina, Uropodina, Prostigmata and Astigmata.

## Results

### Species composition

Seventy-two species were observed at Spikbole (cf. Appendix 2), of which 25 belonged to Mesostigmata, 25 to Prostigmata, 20 to Cryptostigmata and 2 to Astigmata. The number of species is probably underestimated, since many of the larval and nymphal stages were not identified, and neither were some of the adult Prostigmata. Some species were not adequately separated on all sampling occasions, and have been pooled in the following tables. Such species were *Amblyseius okanagensis* (Chant) and *A. obtusus* (C.L.K.), which were approximately equally abundant according to the Tullgren funnel extractions. *Pergamasus runcatellus* (Berl.) and *P. lapponicus* Träg. were difficult to separate in the routine examinations, and were treated together as *P. lapponicus* coll. Close examination of the individuals on two sampling occasions showed that about 95 % of *P. lapponicus* coll. actually belonged to *P. lapponicus* s. str., and thus only 5 % belonged to *P. runcatellus*. Two Brachychthoniidae species, *Brachychochthonius immaculatus* (Forssl.) and *Liochthonius sellnicki* (Thor), were found at Spikbole in the August, October and "winter" samples. The species were not separated on the other sampling occasions. *Oppia minus* (Paoli) and *O. nova* (Oudms) were separated in August, October, November and during the "winter", but not on the other occasions.

### Vertical distribution

The vertical distributions of total Acari and the four main taxonomic groups are illustrated in Fig. 22. More than 70 % of the total number of Acari were, like Collembola, found in the litter and the top 5 cm of the peat soil during May to October. In November the proportion was 60 % and in the "winter" only 40 %. The median depth of the vertical distribution of Acari was about 2 cm from May to October, while it had increased to 2.5 in November and was about 9 cm during the "winter". Two density maxima were observed in the vertical distribution of total Acari in the November and "winter" samples. On both occasions the more shallow maximum was in the litter and upper 2 cm of the soil, while the deeper maximum was at about 8–14 cm in November and at 18–24 cm during the "winter". The astigmatids were exclusively concentrated to the litter and the uppermost 5 cm, while members of the other three groups were also found at deeper levels. Prostigmata generally occurred at a greater mean depth than Meso- and Cryptostigmata and, with the exception of the June sampling, Prostigmata dominated numerically in the soil below the 5 cm level.

Large Mesostigmata, Prostigmata and Cryptostigmata species were confined to the litter layer and the upper topsoil, e.g. most *Pergamasus* spp., *Veigaia* spp., *Dinychus* sp., *Rhagidia* sp., ?*Hauptmannia* sp. and *Trichoribates trimaculatus* (C.L.K.) The astigmatid *Schwiebea cavernicola* Vitzthum and the oribatid *Tectocepheus sarekensis* Träg. were dominant species at the 0–2.5 cm level of the peat soil, but they were also frequently found in the litter and at the 2.5–5 cm level. Other species found at the 0–5 cm depths were *Pergamasus misellus* Berl., *Histiostoma* cf. *feroniarum* (Dufour), Tarsonemidae spp. and other Prostigmata. *Brachychochthonius immaculatus* and *Liochthonius sellnicki* also contributed significantly to the mite density at the 0–2.5 cm level, but their median depths were somewhat greater than that of *T. sarekensis*, and juvenile *B. immaculatus* were found down to about 10 cm. The small mesostigmatid species *Arctoseius cetratus*

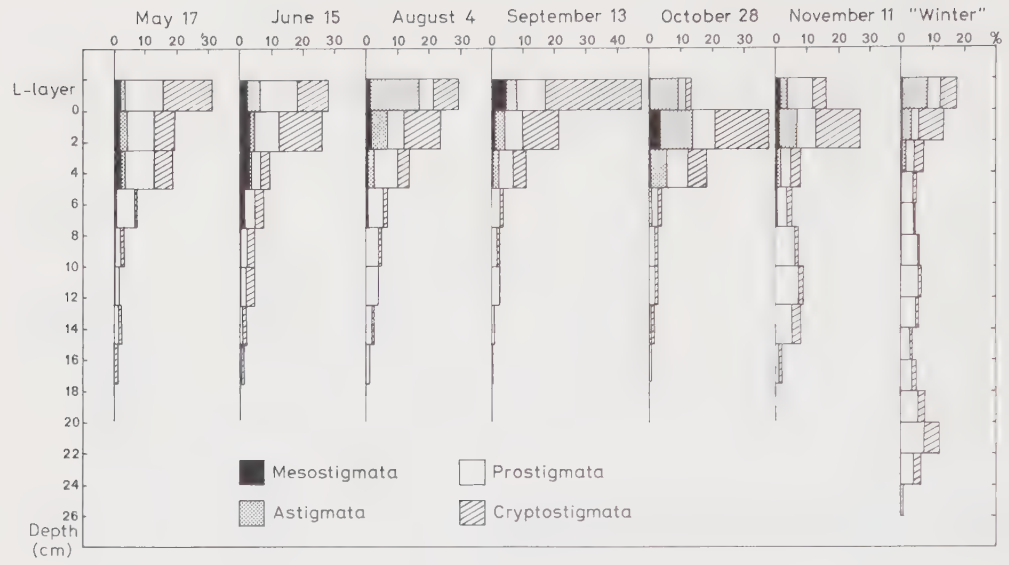


**Figure 22.** The vertical distribution of Acari in 1971–72. The numbers of mites per 2 cm vertical layers are expressed as percentages of the total number on each sampling occasion. L = litter.

(Selln.), *A. insularis* (Willm.) and *Mixozercon sellnicki* (Schw.) had a vertical distribution similar to that of the brachychthoniids and thus occurred in the upper 10 cm of the soil with a density maximum at about 2–4 cm level. The oribatid *Oppia nova* was generally found somewhat deeper than the brachychthoniids, and *Rhodacarellus silesiacus* Willm., Pyemotidae sp., *Scutacarus* sp., *Nanorchestes arboriger* (Berl.), unidentified Prostigmata and *Oppia minus* were observed at depths even deeper than 15 cm. The great changes in vertical distribution between most of the "summer" samplings on one hand and the November and "winter" samplings on the other resembled those of Collembola, but the changes could not be assigned to a single dominant species. The mites mainly responsible for the increasing mean depths were *Scutacarus* sp., unidentified Prostigmata, *Oppia nova* and *O. minus*. The deeper density maximum during the "winter" was caused by juvenile Prostigmata and *O. minus* in particular.

### Abundance

The abundances of the Acari species during the main study period, including the complementary August sampling, are presented in Tables 43–45. Table 43 shows the abundance of Mesostigmata, among which the gamasids were much more numerous than the uropodids. The gamasids *Mixozercon sellnicki, Rhodacarellus silesiacus, Arctoseius insularis* and *Pergamasus lapponicus* coll. were the most dominant species with annual mean densities of 1700 (*s.e.* = 400), 1300 (*s.e.* = 900), 1100 (*s.e.* = 250) and 520 (*s.e.* = 140) $m^{-2}$, respectively. The latter estimate, however, is only valid for adult *P. lapponicus* coll., since juvenile *Pergamasus* were not separated into species. Most of the

Table 43. Abundance (no. $m^{-2}$) of Mesostigmata in 1971–72. The August values are not used for calculating "summer" and annual means. Standard error is given within parentheses below the corresponding mean value.
$N_2$ = deutonymph
M = Macfadyen high gradient canister extraction
T = Tullgren funnel extraction

| | | | May 17 | June 15 | Aug 4 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pachylaelaps* cf. *laeuchlii* | ad | (M+T) | 0 | 0 | 0 | 16<br>(16) | 0 | 0 | 3.2<br>(3.2) | 0 | 2.1<br>(2.1) |
| *Hypoaspis nolli* | juv | (M) | 190<br>(190) | 0 | 0 | 0 | 0 | 0 | 37<br>(37) | 0 | 25<br>(25) |
| *H. nolli* | ad | (M) | 62<br>(62) | 62<br>(62) | 120<br>(85) | 120<br>(85) | 0 | 0 | 49<br>(24) | 63<br>(43) | 54<br>(21) |
| *H.* sp. | ad | (M) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 74<br>(74) | 25<br>(25) |
| *Amblyseius obtusus/ okanagensis* | ad | (M) | 62<br>(62) | 62<br>(62) | 62<br>(62) | 62<br>(62) | 0 | 120<br>(85) | 62<br>(20) | 0 | 41<br>(13) |
| *Lasioseius berlesei* | juv | (M) | 62<br>(62) | 0 | 0 | 0 | 0 | 0 | 12<br>(12) | 0 | 8.2<br>(8.2) |
| *L. berlesei* | ad | (M) | 62<br>(62) | 0 | 0 | 0 | 0 | 0 | 12<br>(12) | 0 | 8.2<br>(8.2) |
| *Cheiroseius borealis* | juv+ad | (M+T) | 0 | 5.3<br>(5.3) | 0 | 64<br>(49) | 0 | 5.3<br>(5.3) | 15<br>(13) | 17<br>(13) | 16<br>(9.2) |
| *Arctoseius cetratus* | juv+ad | (M) | 310<br>(200) | 62<br>(62) | 310<br>(180) | 430<br>(320) | 62<br>(62) | 62<br>(62) | 190<br>(79) | 1 400<br>(500) | 570<br>(180) |
| *A. insularis* | juv | (M) | 0 | 800<br>(380) | 490<br>(440) | 430<br>(320) | 62<br>(62) | 310<br>(310) | 320<br>(150) | 31<br>(31) | 220<br>(97) |
| *A. insularis* | ad | (M) | 310<br>(120) | 62<br>(62) | 740<br>(260) | 1 700<br>(690) | 1 200<br>(400) | 800<br>(360) | 800<br>(290) | 1 000<br>(450) | 870<br>(250) |
| *Mixozercon sellnicki* | juv | (M) | 0 | 1 400<br>(860) | 62<br>(62) | 190<br>(140) | 0 | 190<br>(99) | 350<br>(260) | 480<br>(250) | 390<br>(190) |
| *M. sellnicki* | ad | (M) | 370<br>(160) | 560<br>(410) | 250<br>(110) | 370<br>(180) | 370<br>(220) | 490<br>(440) | 430<br>(40) | 3 000<br>(930) | 1 300<br>(310) |
| *Rhodacarellus silesiacus* | juv+ad | (M) | 490<br>(390) | 6 700<br>(2 500) | 1 500<br>(880) | 310<br>(220) | 62<br>(62) | 120<br>(85) | 1 500<br>(1 300) | 890<br>(400) | 1 300<br>(880) |
| *Dendrolaelaps* sp. | ad | (M) | 250<br>(250) | 0 | 0 | 0 | 0 | 0 | 49<br>(49) | 74<br>(74) | 58<br>(42) |
| *Cyrtolaelaps mucronatus* | $N_2$ | (M+T) | 0 | 0 | 0 | 0 | 5.3<br>(5.3) | 0 | 1.1<br>(1.1) | 0 | 0.7<br>(0.7) |
| *Holoparasitus excipuliger* | juv | (M) | 0 | 370<br>(200) | 62<br>(62) | 0 | 0 | 0 | 74<br>(74) | 0 | 49<br>(49) |
| *H. excipuliger* | ad | (M+T) | 120<br>(85) | 27<br>(15) | 190<br>(99) | 69<br>(33) | 120<br>(41) | 90<br>(63) | 85<br>(18) | 120<br>(86) | 97<br>(31) |
| *Pergamasus brevicornis* | ad | (M+T) | 370<br>(160) | 53<br>(23) | 0 | 290<br>(66) | 270<br>(56) | 260<br>(37) | 250<br>(53) | 260<br>(72) | 250<br>(43) |
| *P. septentrionalis* | ad | (M+T) | 0 | 5.3<br>(5.3) | 62<br>(62) | 85<br>(24) | 80<br>(23) | 37<br>(27) | 42<br>(18) | 59<br>(19) | 47<br>(14) |
| *P. brevicornis/septentrionalis* | $N_2$ | (M+T) | 0 | 48<br>(23) | 120<br>(85) | 380<br>(72) | 43<br>(18) | 32<br>(8.7) | 100<br>(70) | 38<br>(12) | 79<br>(47) |
| *P. misellus* | ad | (M) | 120<br>(85) | 560<br>(240) | 490<br>(200) | 250<br>(150) | 490<br>(200) | 370<br>(310) | 360<br>(80) | 94<br>(68) | 270<br>(58) |
| *P. lapponicus* coll. | ad | (M) | 1 000<br>(460) | 310<br>(250) | 490<br>(240) | 62<br>(62) | 1 000<br>(400) | 680<br>(350) | 630<br>(200) | 300<br>(120) | 520<br>(140) |
| *P.* spp. | juv | (M) | 310<br>(250) | 1 400<br>(450) | 1 400<br>(360) | 1 100<br>(380) | 1 200<br>(390) | 930<br>(370) | 980<br>(180) | 320<br>(140) | 760<br>(130) |
| *Veigaia kochi* | ad | (M+T) | 0 | 0 | 0 | 5.3<br>(5.3) | 21<br>(12) | 0 | 5.3<br>(4.1) | 4.3<br>(4.3) | 5.0<br>(3.1) |
| *V. nemorensis* | juv | (M) | 0 | 0 | 0 | 0 | 120<br>(120) | 0 | 25<br>(25) | 31<br>(31) | 27<br>(20) |
| *V. nemorensis* | ad | (M) | 0 | 0 | 0 | 0 | 62<br>(62) | 0 | 12<br>(12) | 0 | 8.2<br>(8.2) |
| *V. cerva* | juv | (M+T) | 0 | 0 | 0 | 0 | 16<br>(16) | 0 | 3.2<br>(3.2) | 0 | 2.1<br>(2.1) |
| *V. cerva* | ad | (M+T) | 0 | 0 | 0 | 0 | 59<br>(43) | 48<br>(48) | 21<br>(14) | 0 | 14<br>(8.7) |
| Gamasina sp. | juv | (M) | 310<br>(150) | 1 800<br>(450) | 1 000<br>(390) | 740<br>(560) | 0 | 310<br>(310) | 630<br>(320) | 0 | 420<br>(210) |
| Gamasina, total | | (M+T) | 4 400<br>(890) | 14 200<br>(2 800) | 7 500<br>(1 400) | 6 600<br>(1 300) | 5 200<br>(800) | 4 900<br>(950) | 7 100<br>(1 900) | 8 200<br>(1 200) | 7 400<br>(1 300) |
| *Dinychus* sp. | juv | (M+T) | 120<br>(85) | 5.3<br>(5.3) | 370<br>(180) | 180<br>(120) | 53<br>(48) | 96<br>(79) | 91<br>(30) | 34<br>(24) | 72<br>(21) |
| *D.* sp. | ad | (M+T) | 62<br>(62) | 0 | 0 | 120<br>(76) | 150<br>(98) | 74<br>(54) | 83<br>(27) | 84<br>(44) | 83<br>(23) |
| Uropodina sp. | juv+ad | (M+T) | 0 | 5.3<br>(5.3) | 0 | 11<br>(11) | 0 | 0 | 3.2<br>(2.2) | 15<br>(6.6) | 7.2<br>(2.7) |
| Uropodina, total | | (M+T) | 190<br>(140) | 11<br>(7.1) | 370<br>(180) | 310<br>(160) | 210<br>(150) | 170<br>(82) | 180<br>(48) | 130<br>(62) | 160<br>(38) |

*Pergamasus* juveniles probably belonged to *P. lapponicus* coll. and consequently the total abundance of this species should amount to about 1000 $m^{-2}$, most of which were probably *P. lapponicus* s. str. specimens. *Dinychus* sp. was the predominant Uropodina species with 150 (*s.e.* = 40) individuals $m^{-2}$ as an annual average. The lowest density of total Gamasina was obtained in May, when most of the specimens were adults, while the highest abundance was recorded in June. The high density on that occasion coincided with the occurrence of a high proportion of juveniles belonging to, for example, *M. sellnicki*, *A. insularis* and *Pergamasus* spp. Generally most juveniles were found in June and August, after which the ratio of juveniles/adults decreased towards the winter. The annual mean abundance was estimated at 7400 (*s.e.* = 1300) $m^{-2}$ for total Gamasina and 160 (*s.e.* = 38) $m^{-2}$ for Urpodina.

A considerable amount of the Prostigmata specimens belonged to the families Eupodidae, Rhagidiidae, Tetranychidae and Tydeidae, among others, which however were pooled as Prostigmata sp. due to the taxonomic problems (Table 44). Pyemotidae, Scutacaridae and Tarsonemidae were also relatively abundant. The annual mean abundance of total Prostigmata was estimated at 51 000 (*s.e.* = 5800) $m^{-2}$.

Table 44. Abundance (no. $m^{-2}$) of Prostigmata and Astigmata in 1971–72. The August values are not used for calculating "summer" and annual means. Standard error is given within parentheses below the corresponding mean value
M = Macfadyen high gradient canister extraction
T = Tullgren funnel extraction

| | | | May 17 | June 15 | Aug 4 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Pyemotidae spp. | juv+ad | (M) | 2 000<br>(550) | 1 400<br>(410) | 2 800<br>(1 600) | 5 100<br>(2 000) | 6 300<br>(4 800) | 8 600<br>(2 600) | 4 700<br>(1 400) | 7 300<br>(2 100) | 5 600<br>(1 200) |
| *Scutacarus* spp. | juv+ad | (M) | 4 800<br>(2 000) | 2 000<br>(690) | 1 800<br>(630) | 1 500<br>(490) | 2 300<br>(680) | 1 600<br>(870) | 2 400<br>(600) | 3 700<br>(880) | 2 900<br>(500) |
| Tarsonemidae sp. | juv+ad | (M) | 740<br>(230) | 1 400<br>(450) | 2 100<br>(800) | 4 100<br>(1 100) | 4 300<br>(960) | 6 000<br>(1 400) | 3 300<br>(990) | 2 200<br>(420) | 2 900<br>(670) |
| Eriophyidae sp. | juv+ad | (M) | 0 | 62<br>(62) | 120<br>(84) | 120<br>(84) | 0 | 1 100<br>(700) | 260<br>(220) | 130<br>(72) | 210<br>(150) |
| Anystidae sp. | ad | (M+T) | 0 | 0 | 0 | 27<br>(15) | 0 | 0 | 5.3<br>(5.3) | 0 | 3.5<br>(3.5) |
| Prostigmata spp. | juv+ad | (M) | 16 900<br>(3 000) | 25 300<br>(3 400) | 53 200<br>(15 700) | 13 900<br>(2 300) | 12 000<br>(2 100) | 33 600<br>(10 000) | 20 300<br>(4 100) | 76 000<br>(13 200) | 38 900<br>(5 200) |
| Prostigmata, total | | (M+T) | 24 300<br>(3 500) | 30 200<br>(4 000) | 60 000<br>(16 500) | 24 800<br>(4 500) | 24 900<br>(5 400) | 51 000<br>(10 800) | 31 000<br>(5 100) | 89 300<br>(14 200) | 50 500<br>(5 800) |
| *Histiostoma* cf. *feroniarum* | juv+ad | (M) | 680<br>(250) | 860<br>(350) | 2 500<br>(1 100) | 3 500<br>(1 100) | 930<br>(340) | 1 800<br>(550) | 1 500<br>(520) | 1 900<br>(540) | 1 700<br>(390) |
| *Schwiebea cavernicola* | juv+ad | (M) | 1 900<br>(1 200) | 5 700<br>(4 200) | 33 200<br>(15 600) | 4 800<br>(1 600) | 23 300<br>(6 900) | 8 600<br>(4 500) | 8 900<br>(3 800) | 21 000<br>(5 900) | 12 900<br>(3 200) |
| Astigmata sp. | juv | (M) | 0 | 120<br>(84) | 0 | 0 | 0 | 0 | 25<br>(25) | 31<br>(31) | 27<br>(20) |
| Astigmata, total | | (M) | 2 500<br>(1 300) | 6 700<br>(4 200) | 35 700<br>(16 000) | 8 300<br>(2 000) | 24 300<br>(6 900) | 10 400<br>(4 400) | 10 400<br>(3 700) | 23 000<br>(6 000) | 14 600<br>(3 200) |

Table 45. Abundance (no. $m^{-2}$) of Cryptostigmata and total Acari in 1971–72. The August values are not used for calculating "summer" and annual means. Standard error is given within parentheses below the corresponding mean value.
M = Macfadyen high gradient canister extraction
T = Tullgren funnel extraction

| | | | May 17 | June 15 | Aug 4 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Steganacarus striculus* | ad | (M+T) | 0 | 0 | 62<br>(62) | 11<br>(7.1) | 0 | 0 | 2.1<br>(2.1) | 0 | 1.4<br>(1.4) |
| *Hypochthonius rufulus* | ad | (M) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 31<br>(31) | 10<br>(10) |
| Brachychthoniidae spp. | juv | (M) | 1 200<br>(190) | 10 300<br>(4 400) | 25 200<br>(6 200) | 14 100<br>(3 800) | 5 000<br>(1 300) | 7 900<br>(1 900) | 7 700<br>(2 200) | 7 000<br>(1 200) | 7 500<br>(1 600) |
| B. spp. | ad | (M) | 4 600<br>(1 200) | 4 000<br>(1 300) | 1 100<br>(360) | 13 800<br>(2 700) | 9 400<br>(2 400) | 9 000<br>(2 000) | 8 100<br>(1 800) | 12 000<br>(2 300) | 9 400<br>(1 500) |
| *Platynothrus peltifer* | juv | (M+T) | 0 | 0 | 0 | 0 | 0 | 21<br>(21) | 4.3<br>(4.3) | 23<br>(22) | 11<br>(7.7) |
| *P. peltifer* | ad | (M+T) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.8<br>(1.8) | 1.2<br>(1.2) |
| *Damaeus clavipes* | ad | (M+T) | 0 | 0 | 0 | 0 | 0 | 5.3<br>(5.3) | 1.1<br>(1.1) | 0 | 0.7<br>(0.7) |
| *D. verticillipes* | juv | (M+T) | 0 | 0 | 0 | 0 | 11<br>(11) | 117<br>(117) | 26<br>(23) | 0 | 17<br>(16) |
| *D. verticillipes* | ad | (M+T) | 0 | 0 | 62<br>(62) | 0 | 5.3<br>(5.3) | 32<br>(27) | 7.4<br>(6.2) | 0 | 4.9<br>(4.1) |
| *Carabodes areolatus* | ad | (M) | 0 | 0 | 0 | 62<br>(62) | 0 | 0 | 12<br>(12) | 0 | 8.2<br>(8.2) |
| *Tectocepheus sarekensis* | juv | (M) | 4 500<br>(1 000) | 4 500<br>(1 700) | 6 500<br>(2 000) | 8 400<br>(2 000) | 6 900<br>(1 600) | 5 000<br>(1 300) | 5 900<br>(770) | 5 400<br>(710) | 5 700<br>(570) |
| *T. sarekensis* | ad | (M) | 3 300<br>(860) | 4 500<br>(1 300) | 4 600<br>(790) | 3 600<br>(700) | 2 800<br>(730) | 2 300<br>(830) | 3 300<br>(370) | 3 100<br>(620) | 3 300<br>(320) |
| *Oppia minus/nova* | juv | (M) | 370<br>(160) | 0 | 800<br>(200) | 120<br>(85) | 250<br>(150) | 1 700<br>(800) | 490<br>(320) | 4 900<br>(1 900) | 1 900<br>(660) |
| *O. minus/nova* | ad | (M) | 3 000<br>(470) | 13 100<br>(3 300) | 3 400<br>(980) | 1 400<br>(480) | 2 600<br>(610) | 7 100<br>(3 000) | 5 400<br>(2 200) | 19 000<br>(4 100) | 10 000<br>(2 000) |
| *Suctobelba subtrigona* | ad | (M) | 0 | 0 | 0 | 0 | 123<br>(123) | 0 | 25<br>(25) | 0 | 16<br>(16) |
| *Oribatula tibialis* | ad | (M) | 0 | 0 | 0 | 0 | 0 | 62<br>(62) | 12<br>(12) | 0 | 8.2<br>(8.2) |
| *Hemileius initialis* | ad | (M) | 0 | 0 | 0 | 0 | 62<br>(62) | 0 | 12<br>(12) | 140<br>(86) | 54<br>(30) |
| *Scheloribates laevigatus* | ad | (M) | 0 | 0 | 62<br>(62) | 0 | 0 | 0 | 0 | 74<br>(74) | 25<br>(25) |
| *Chamobates cuspidatus* | ad | (M) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 220<br>(110) | 74<br>(35) |
| *Trichoribates trimaculatus* | juv | (M+T) | 62<br>(62) | 90<br>(42) | 190<br>(140) | 170<br>(53) | 1 400<br>(620) | 910<br>(210) | 520<br>(270) | 1 800<br>(380) | 940<br>(220) |
| *T. trimaculatus* | ad | (M+T) | 62<br>(62) | 180<br>(71) | 120<br>(120) | 220<br>(78) | 260<br>(84) | 110<br>(23) | 170<br>(37) | 180<br>(34) | 170<br>(27) |
| *Neoribates aurantiacus* | ad | (M+T) | 0 | 0 | 0 | 130<br>(63) | 350<br>(270) | 130<br>(110) | 120<br>(65) | 19<br>(11) | 88<br>(43) |
| Cryptostigmata sp. | juv | (M) | 0 | 190<br>(99) | 62<br>(62) | 0 | 0 | 0 | 37<br>(37) | 31<br>(31) | 35<br>(27) |
| Cryptostigmata, total | | (M+T) | 17 200<br>(2 100) | 36 800<br>(6 900) | 42 100<br>(6 400) | 42 100<br>(6 500) | 29 200<br>(3 200) | 34 400<br>(4 800) | 31 900<br>(4 300) | 53 900<br>(5 900) | 39 200<br>(3 500) |
| Acari, total | | (M+T) | 48 600<br>(4 200) | 87 900<br>(11 800) | 145 700<br>(24 400) | 82 100<br>(9 700) | 83 800<br>(11 400) | 100 900<br>(13 400) | 80 700<br>(8 700) | 174 500<br>(18 100) | 111 900<br>(8 400) |

*Schwiebea cavernicola* was the predominant species among Astigmata, and its annual mean abundance was estimated at 13 000 (*s.e.* = 3200) $m^{-2}$. The horizontal distribution of this species seemed to be very aggregated, causing a fairly low precision in the estimates. The numbers of total Astigmata varied between 2500 (*s.e.* = 1300) $m^{-2}$ in May and 36 000 (*s.e.* = 16 000) $m^{-2}$ in August, but due to the low precision no seasonal trend could be found. The annual mean abundance was about 15 000 (*s.e.* = 3200) $m^{-2}$ for total Astigmata. Hypopial nymphs of both *S. cavernicola* and *Histiostoma* cf. *feroniarum* were found in the soil samples, but this non-feeding stage contributed insignificantly to the total abundance of Astigmata.

The abundances of Cryptostigmata and total Acari are presented in Table 45. Brachychthoniidae spp., *Oppia* spp. and *Tectocepheus sarekensis* were the most numerous oribatids with annual mean abundances of 17 000 (*s.e.* = 2600), 12 000 (*s.e.* = 2400) and 9000 (*s.e.* = 700) specimens $m^{-2}$, respectively. *Brachychochthonius immaculatus* accounted for somewhat more than 80 % and *Liochthonius sellnicki* for somewhat less than 20 % of adult Brachychthoniidae at the August, October and "winter" samplings. Assuming the same proportion at the other samplings and also for the juveniles, the abundance of *B. immaculatus* was about 14 000 $m^{-2}$ in comparison with 3000 $m^{-2}$ for *L. sellnicki*. The corresponding values for *Oppia minus* and *O. nova* based on the adults at the August, October, November and "winter" samplings were 7500 and 4500 $m^{-2}$, respectively. The highest abundances of total Cryptostigmata during the "summer" period were estimated at about 42 000 $m^{-2}$ both in August and September, when Brachychthoniidae accounted for more than 60 % of the total number. About 96 % of the brachychthoniids were juveniles in August, but this large proportion decreased significantly to about 50 % in September, after which the number of adults became higher than that of the juveniles. The relationship between juvenile and adult *T. sarekensis* changed much less over the year, and the greatest percentage of juveniles was found during September and October. The number of juvenile *Oppia* spp. was very small on all sampling occasions in relation to the number of adults. Thus, there was no unanimous trend in the relationship between juvenile and adult Cryptostigmata, but the dominance of Brachychthoniidae meant that the highest proportion of juvenile oribatids was obtained in August. The proportion decreased successively towards the "winter", when only 36 % were juveniles, and the same proportion was also obtained in May.

The annual mean abundance of total Acari was estimated at 112 000 (*s.e.* = 8400) specimens $m^{-2}$ (Table 45), to which Mesostigmata, Prostigmata, Astigmata and Cryptostigmata contributed about 7600, 51 000, 15 000 and 39 000 individuals $m^{-2}$, respectively.

### Biomass

The biomasses of the different Acari species and other taxa are given in Tables 46–48, of which Table 46 shows the biomasses of Gamasina and Uropodina. The larger Gamasina species contributed much more to the total biomass than the smaller but more abundant species. The annual mean biomass for the large-sized (cf. Table 40) *Pergamasus brevicornis* Berl. was estimated at 23 (*s.e.* = 3.9) mg dw $m^{-2}$ for the adult stage. The other large *Pergamasus* species, *P. septentrionalis* (Oudms) accounted for 5.7 (*s.e.* = 1.7) mg $m^{-2}$ in the adult stage. The annual mean biomass of adults and deutonymphs of these two species was estimated at about 33 mg dw $m^{-2}$, and together with the

Table 46. Biomass (mg dry weight $m^{-2}$) of Mesostigmata in 1971–72. The August values are not used for calculating "summer" and annual means. Standard error is given within parentheses below the corresponding mean value.
$N_2$ = deutonymph

| | | May 17 | June 15 | Aug 4 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|---|
| *Pachylaelaps* cf. *laeuchlii* | ad | 0 | 0 | 0 | 0.54 (0.54) | 0 | 0 | 0.11 (0.11) | 0 | 0.07 (0.07) |
| *Hypoaspis nolli* | juv | 0.37 (0.37) | 0 | 0 | 0 | 0 | 0 | 0.07 (0.07) | 0 | 0.05 (0.05) |
| *H. nolli* | ad | 0.40 (0.40) | 0.40 (0.40) | 0.80 (0.55) | 0.80 (0.55) | 0 | 0 | 0.32 (0.15) | 0.41 (0.28) | 0.35 (0.14) |
| *H.* sp. | ad | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.48 (0.48) | 0.16 (0.16) |
| *Amblyseius obtusus/okanagensis* | ad | 0.26 (0.26) | 0.26 (0.26) | 0.26 (0.26) | 0.26 (0.26) | 0 | 0.52 (0.35) | 0.26 (0.09) | 0 | 0.17 (0.06) |
| *Lasioseius berlesei* | juv | 0.48 (0.48) | 0 | 0 | 0 | 0 | 0 | 0.10 (0.10) | 0 | 0.07 (0.07) |
| *L. berlesei* | ad | 0.16 (0.16) | 0 | 0 | 0 | 0 | 0 | 0.03 (0.03) | 0 | 0.02 (0.02) |
| *Cheiroseius borealis* | juv+ad | 0 | 0.03 (0.03) | 0 | 0.41 (0.32) | 0 | 0.03 (0.03) | 0.10 (0.08) | 0.11 (0.09) | 0.10 (0.06) |
| *Arctoseius cetratus* | juv+ad | 0.65 (0.41) | 0.13 (0.13) | 0.65 (0.37) | 0.91 (0.66) | 0.13 (0.13) | 0.13 (0.13) | 0.39 (0.17) | 2.84 (1.03) | 1.20 (0.36) |
| *A. insularis* | juv | 0 | 0.56 (0.26) | 0.35 (0.31) | 0.30 (0.22) | 0.04 (0.04) | 0.22 (0.22) | 0.22 (0.10) | 0.02 (0.02) | 0.16 (0.07) |
| *A. insularis* | ad | 0.65 (0.25) | 0.13 (0.13) | 1.56 (0.55) | 3.50 (1.45) | 2.46 (0.84) | 1.69 (0.76) | 1.69 (0.61) | 2.12 (0.93) | 1.83 (0.51) |
| *Mixozercon sellnicki* | juv | 0 | 0.95 (0.60) | 0.04 (0.04) | 0.13 (0.10) | 0 | 0.13 (0.07) | 0.24 (0.18) | 0.34 (0.18) | 0.27 (0.14) |
| *M. sellnicki* | ad | 0.81 (0.39) | 1.22 (0.89) | 0.54 (0.24) | 0.81 (0.39) | 0.81 (0.48) | 1.09 (0.95) | 0.95 (0.09) | 6.52 (2.04) | 2.81 (0.69) |
| *Rhodacarellus silesiacus* | juv+ad | 0.49 (0.39) | 6.73 (2.44) | 1.54 (0.88) | 0.31 (0.22) | 0.06 (0.06) | 0.12 (0.09) | 1.54 (1.30) | 0.89 (0.41) | 1.33 (0.88) |
| *Dendrolaelaps* sp. | ad | 0.52 (0.52) | 0 | 0 | 0 | 0 | 0 | 0.10 (0.10) | 0.16 (0.16) | 0.12 (0.09) |
| *Cyrtolaelaps mucronatus* | $N_2$ | 0 | 0 | 0 | 0 | 0.13 (0.13) | 0 | 0.03 (0.03) | 0 | 0.02 (0.02) |
| *Holoparasitus excipuliger* | juv | 0 | 2.96 (1.59) | 0.49 (0.49) | 0 | 0 | 0 | 0.59 (0.59) | 0 | 0.39 (0.39) |
| *H. excipuliger* | ad | 3.08 (2.10) | 0.67 (0.36) | 4.63 (2.48) | 1.73 (0.82) | 2.93 (1.01) | 2.26 (1.57) | 2.13 (0.44) | 3.03 (2.13) | 2.43 (0.77) |
| *Pergamasus brevicornis* | ad | 33.33 (13.61) | 4.79 (2.02) | 0 | 25.85 (5.94) | 23.94 (5.00) | 22.98 (3.33) | 22.18 (4.72) | 23.27 (6.44) | 22.55 (3.81) |
| *P. septentrionalis* | ad | 0 | 0.64 (0.64) | 7.41 (7.41) | 10.21 (2.89) | 9.57 (2.73) | 4.47 (3.16) | 4.98 (2.15) | 7.11 (2.23) | 5.69 (1.62) |
| *P. brevicornis/septentrionalis* | $N_2$ | 0 | 2.63 (1.27) | 6.79 (4.63) | 20.77 (3.91) | 2.34 (0.96) | 1.76 (0.48) | 5.50 (3.84) | 2.09 (0.63) | 4.36 (2.57) |
| *P. misellus* | ad | 0.89 (0.61) | 4.00 (1.70) | 3.56 (1.44) | 1.78 (1.03) | 3.56 (1.44) | 2.67 (2.24) | 2.58 (0.57) | 0.68 (0.49) | 1.94 (0.42) |
| *P. lapponicus* coll. | ad | 20.99 (9.19) | 6.18 (5.00) | 9.88 (4.74) | 1.23 (1.23) | 20.99 (7.85) | 13.58 (6.87) | 12.59 (3.95) | 6.10 (2.41) | 10.43 (2.75) |
| *P.* spp. | juv | 1.85 (1.50) | 8.15 (2.70) | 8.52 (2.16) | 6.67 (2.25) | 7.04 (2.33) | 5.56 (2.17) | 5.85 (1.08) | 1.95 (0.79) | 4.55 (0.77) |
| *Veigaia kochi* | ad | 0 | 0 | 0 | 0.48 (0.48) | 1.92 (1.06) | 0 | 0.48 (0.37) | 0.38 (0.38) | 0.45 (0.28) |
| *V. nemorensis* | juv | 0 | 0 | 0 | 0 | 0.74 (0.74) | 0 | 0.15 (0.15) | 0.19 (0.19) | 0.16 (0.12) |
| *V. nemorensis* | ad | 0 | 0 | 0 | 0 | 1.05 (1.05) | 0 | 0.21 (0.21) | 0 | 0.14 (0.14) |
| *V. cerva* | juv | 0 | 0 | 0 | 0 | 0.16 (0.16) | 0 | 0.03 (0.03) | 0 | 0.02 (0.02) |
| *V. cerva* | ad | 0 | 0 | 0 | 0 | 1.76 (1.27) | 1.44 (1.44) | 0.64 (0.40) | 0 | 0.43 (0.27) |
| Gamasina sp. | juv | 0.62 (0.30) | 3.58 (0.90) | 2.10 (0.77) | 1.48 (1.11) | 0 | 0.62 (0.62) | 1.26 (0.63) | 0 | 0.84 (0.42) |
| Gamasina, total | | 65.55 | 44.01 | 49.12 | 78.17 | 79.63 | 59.27 | 65.33 (6.56) | 58.69 (6.85) | 63.12 (4.94) |
| *Dinychus* sp. | ad | 1.85 (1.85) | 0 | 0 | 3.67 (2.29) | 4.63 (2.94) | 2.23 (1.62) | 2.48 (0.80) | 2.52 (1.30) | 2.49 (0.69) |
| *D.* sp. | juv | 0.99 (0.68) | 0.04 (0.04) | 2.96 (1.41) | 1.40 (0.97) | 0.43 (0.39) | 0.77 (0.63) | 0.73 (0.24) | 0.27 (0.19) | 0.58 (0.17) |
| Uropodina sp. | juv+ad | 0 | 0.13 (0.13) | 0 | 0.26 (0.26) | 0 | 0 | 0.08 (0.06) | 0.32 (0.15) | 0.16 (0.07) |
| Uropodina, total | | 2.84 | 0.17 | 2.96 | 5.33 | 5.06 | 3.00 | 3.28 (0.93) | 3.12 (1.42) | 3.23 (0.78) |

relatively large *P. lapponicus* coll. with 10 (*s.e.* = 2.8) mg $m^{-2}$ in the adult stage only, these species accounted for about 70 % of the annual mean biomass of total Gamasina which was estimated at 63 (*s.e.* = 5.0) mg dw $m^{-2}$. The total Gamasina biomass varied between 44 mg $m^{-2}$ in June and 80 mg $m^{-2}$ in October. The annual mean biomass of total Uropodina was estimated at 3.2 (*s.e.* = 0.8) mg dw $m^{-2}$.

The biomasses of total Prostigmata and total Astigmata (Table 47) were considerably smaller than that of total Gamasina, reflecting the lower mean body weights. The annual mean biomass of total Prostigmata was estimated at 15 (*s.e.* = 1.8) mg $m^{-2}$, but this estimate is uncertain because of the difficulty to choose a correct mean body weight for animals of different sizes. The annual mean biomass of total Astigmata was estimated at 10 (*s.e.* = 2.3) mg dw $m^{-2}$, to which *Schwiebea cavernicola* contributed 9.3 (*s.e.* = 2.3) mg $m^{-2}$.

Table 47. Biomass (mg dry weight $m^{-2}$) of Prostigmata and Astigmata in 1971–72. The August values are not used for calculating "summer" and annual means. Standard error is given within parentheses below the corresponding mean value.

| | | May 17 | June 15 | Aug 4 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|---|
| Pyemotidae spp. | juv+ad | 0.32 (0.09) | 0.23 (0.07) | 0.44 (0.26) | 0.82 (0.32) | 1.01 (0.76) | 1.38 (0.42) | 0.75 (0.22) | 1.17 (0.33) | 0.89 (0.18) |
| *Scutacarus* spp. | juv+ad | 0.76 (0.32) | 0.32 (0.11) | 0.29 (0.10) | 0.25 (0.08) | 0.38 (0.11) | 0.26 (0.14) | 0.39 (0.10) | 0.59 (0.14) | 0.46 (0.08) |
| Tarsonemidae sp. | juv+ad | 0.12 (0.04) | 0.23 (0.07) | 0.34 (0.13) | 0.65 (0.17) | 0.69 (0.16) | 0.97 (0.22) | 0.53 (0.16) | 0.35 (0.07) | 0.47 (0.11) |
| Eriophyidae sp. | juv+ad | 0 | 0.02 (0.02) | 0.04 (0.03) | 0.04 (0.03) | 0 | 0.36 (0.23) | 0.08 (0.07) | 0.04 (0.03) | 0.07 (0.05) |
| Anystidae sp. | ad | 0 | 0 | 0 | 2.39 (1.29) | 0 | 0 | 0.48 (0.26) | 0 | 0.32 (0.17) |
| Prostigmata spp. | juv+ad | 5.39 (0.95) | 8.10 (1.07) | 17.03 (5.02) | 4.44 (0.72) | 3.83 (0.67) | 10.75 (3.18) | 6.50 (1.29) | 24.04 (4.21) | 12.35 (1.65) |
| Prostigmata, total | | 6.59 | 8.90 | 18.14 | 8.59 | 5.91 | 13.72 | 8.74 (1.37) | 26.18 (4.35) | 14.55 (1.72) |
| *Histiostoma* cf. *feroniarum* | juv+ad | 0.31 (0.12) | 0.40 (0.16) | 1.16 (0.48) | 1.59 (0.49) | 0.43 (0.16) | 0.82 (0.26) | 0.71 (0.24) | 0 90 (0.25) | 0.77 (0.18) |
| *Schwiebea cavernicola* | juv+ad | 1.33 (0.82) | 4.09 (2 99) | 23.91 (11.23) | 3.47 (1.14) | 16.80 (4.98) | 6.22 (3.19) | 6.38 (2.72) | 15.13 (4 19) | 9.30 (2.29) |
| Astigmata sp. | juv | 0 | 0.06 (0.04) | 0 | 0 | 0 | 0 | 0.01 (0.01) | 0.01 (0.01) | 0.01 (0 01) |
| Astigmata, total | | 1.65 | 4.54 | 25.08 | 5.06 | 17.23 | 7.05 | 7.10 (2.68) | 16.04 (4.26) | 10.08 (2.29) |

The annual mean biomasses of *Trichoribates trimaculatus* (C.L.K.), *Tectopheus sarekensis*, *Oppia* spp. and Brachychthoniidae spp. were estimated at about 15, 11, 6 and 5 mg dw $m^{-2}$, respectively, and these oribatids were the only ones with a biomass exceeding one mg $m^{-2}$ (Table 48). The annual mean oribatid biomass was estimated at 39 (*s.e.* = 3.1) mg dw $m^{-2}$.

The biomass of total Acari varied between 89 mg $m^{-2}$ in June and 160 mg $m^{-2}$ during the "winter". The annual mean biomass of total Acari was estimated at 130 (*s.e.* = 8.3) mg dw $m^{-2}$, of which Mesostigmata, Prostigmata, Astigmata and Cryptostigmata contributed 66, 15, 10 and 39 mg dw $m^{-2}$, respectively (Table 48).

Table 48. Biomass (mg dry weight $m^{-2}$) of Cryptostigmata and total Acari in 1971–72. The August values are not used for calculating "summer" and annual means. Standard error is given within parentheses below the corresponding mean value.

| | | May 17 | June 15 | Aug 4 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|---|
| *Steganacarus striculus* | ad | 0 | 0 | 0.62 (0.62) | 0.11 (0.08) | 0 | 0 | 0.02 (0.02) | 0 | 0.01 (0.01) |
| *Hypochthonius rufulus* | ad | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.34 (0.34) | 0.11 (0.11) |
| Brachychthoniidae spp. | juv | 0.12 (0.02) | 1.03 (0.45) | 2.52 (0.62) | 1.41 (0.38) | 0.50 (0.13) | 0.79 (0.19) | 0.77 (0.22) | 0.70 (0.12) | 0.75 (0.16) |
| B. spp. | ad | 1.83 (0.46) | 1.58 (0.50) | 0.44 (0.15) | 5.51 (1.06) | 3.78 (0.96) | 3.58 (0.77) | 3.25 (0.72) | 4.81 (0.92) | 3.77 (0.57) |
| *Platynothrus peltifer* | juv | 0 | 0 | 0 | 0 | 0 | 0.12 (0.12) | 0.02 (0.02) | 0.13 (0.12) | 0.06 (0.05) |
| *P. peltifer* | ad | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.04 (0.04) | 0.01 (0.01) |
| *Damaeus clavipes* | ad | 0 | 0 | 0 | 0 | 0 | 0.47 (0.47) | 0.09 (0.09) | 0 | 0.06 (0.06) |
| *D. verticillipes* | juv | 0 | 0 | 0 | 0 | 0.12 (0.12) | 1.38 (1.38) | 0.30 (0.27) | 0 | 0.20 (0.18) |
| *D. verticillipes* | ad | 0 | 0 | 2.90 (2.90) | 0 | 0.25 (0.25) | 1.50 (1.25) | 0.35 (0.30) | 0 | 0.23 (0.20) |
| *Carabodes areolatus* | ad | 0 | 0 | 0 | 0.49 (0.49) | 0 | 0 | 0.10 (0.10) | 0 | 0.07 (0.07) |
| *Tectocepheus sarekensis* | juv | 2.70 (0.61) | 2.70 (1.03) | 3.89 (1.17) | 5.04 (1.19) | 4.11 (0.93) | 3.00 (0.74) | 3.51 (0.47) | 3.26 (0.43) | 3.43 (0.34) |
| *T. sarekensis* | ad | 8.00 (2.06) | 10.81 (3.04) | 11.11 (1.88) | 8.74 (1.68) | 6.82 (1.75) | 5.63 (1.98) | 8.00 (0.88) | 7.52 (1.48) | 7.84 (0.77) |
| *Oppia minus/nova* | juv | 0.06 (0.03) | 0 | 0.12 (0.03) | 0.02 (0.02) | 0.04 (0.03) | 0.26 (0.12) | 0.07 (0.05) | 0.73 (0.28) | 0.29 (0.10) |
| *O. minus/nova* | ad | 1.82 (0.28) | 7.85 (1.96) | 2.04 (0.59) | 0.85 (0.29) | 1.56 (0.37) | 4.26 (1.81) | 3.27 (1.29) | 11.40 (2.44) | 5.98 (1.18) |
| *Suctobelba subtrigona* | ad | 0 | 0 | 0 | 0 | 0.12 (0.12) | 0 | 0.02 (0.02) | 0 | 0.02 (0.02) |
| *Oribatula tibialis* | ad | 0 | 0 | 0 | 0 | 0 | 0.37 (0.37) | 0.07 (0.07) | 0 | 0.05 (0.05) |
| *Hemileius initialis* | ad | 0 | 0 | 0 | 0 | 0.60 (0.60) | 0 | 0.12 (0.12) | 1.33 (0.83) | 0.52 (0.29) |
| *Scheloribates laevigatus* | ad | 0 | 0 | 1.05 (1.05) | 0 | 0 | 0 | 0 | 1.26 (1.26) | 0.42 (0.42) |
| *Chamobates cuspidatus* | ad | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.96 (0.45) | 0.32 (0.15) |
| *Trichoribates trimaculatus* | juv | 0.56 (0.56) | 0.81 (0.38) | 1.67 (1.21) | 1.53 (0.48) | 12.45 (5.56) | 8.19 (1.90) | 4.71 (2.40) | 15.93 (3.41) | 8.45 (1.96) |
| *T. trimaculatus* | ad | 2.22 (2.22) | 6.51 (2.54) | 4.44 (4.44) | 8.04 (2.78) | 9.38 (3.03) | 4.02 (0.83) | 6.04 (1.31) | 6.41 (1.23) | 6.16 (0.96) |
| *Neoribates aurantiacus* | ad | 0 | 0 | 0 | 1.02 (0.49) | 2.70 (2.02) | 0.98 (0.81) | 0.94 (0.50) | 0.14 (0.08) | 0.68 (0.33) |
| Cryptostigmata sp. | juv | 0 | 0.37 (0.20) | 0.12 (0.12) | 0 | 0 | 0 | 0.07 (0.07) | 0.06 (0.06) | 0.07 (0.06) |
| Cryptostigmata, total | | 17.30 | 31.68 | 30.92 | 32.77 | 42.43 | 34.54 | 31.74 (4.07) | 55.01 (3.85) | 39.50 (3.01) |
| Acari, total | | 93.93 | 89.30 | 126.22 | 129.92 | 150.26 | 117.58 | 116.20 (11.34) | 159.03 (10.00) | 130.48 (8.27) |

## Respiration

The oxygen consumption rates and annual respiration of Mesostigmata are presented in Table 49. Adult *Pergamasus brevicornis,* adult *P. lapponicus* coll. and adult *P. septentrionalis* contributed 0.43 (*s.e.* = 0.12), 0.27 (*s.e.* = 0.10) and 0.09 (*s.e.* = 0.04) kcal $m^{-2}$ to the annual Gamasina respiration of 1.5 (*s.e.* = 0.20) kcal $m^{-2}$. The juveniles contributed a higher part of the annual respiration than was indicated by the annual mean biomass due to their higher respiration rates per unit weight and since they occurred most frequently during the warmest season. The respiration of Uropodina was very small in comparison with that of Gamasina.

Table 50 shows the oxygen consumption rates and annual respiration of Prostigmata

Table 49. Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) and annual respiration (kcal $m^{-2}$) of Mesostigmata in 1971–72. The August values are not used for calculating "summer" and annual means. Standard error is given within parentheses below the corresponding mean value. + denotes a value less than 0.0005.
$N_2$ = deutonymph

| | | Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) | | | | | | | | | Annual respiration (kcal $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | May 17 | June 15 | Aug 4 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual | |
| *Pachylaelaps* cf. *laeuchlii* | ad | 0 | 0 | 0 | 0.009 (0.009) | 0 | 0 | 0.002 (0.002) | 0 | 0.001 (0.001) | 0.002 (0.002) |
| *Hypoaspis nolli* | juv | 0.012 (0.012) | 0 | 0 | 0 | 0 | 0 | 0.002 (0.002) | 0 | 0.002 (0.002) | 0.003 (0.003) |
| *H. nolli* | ad | 0.011 (0.011) | 0.011 (0.011) | 0.036 (0.025) | 0.016 (0.011) | 0 | 0 | 0.008 (0.004) | 0.003 (0.002) | 0.006 (0.003) | 0.011 (0.004) |
| *H.* sp. | ad | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.004 (0.004) | 0.001 (0.001) | 0.002 (0.002) |
| *Amblyseius obtusus/okanagensis* | ad | 0.007 (0.007) | 0.007 (0.007) | 0.012 (0.012) | 0.006 (0.006) | 0 | 0.006 (0.004) | 0.005 (0.002) | 0 | 0.003 (0.001) | 0.006 (0.002) |
| *Lasioseius berlesei* | juv | 0.005 (0.005) | 0 | 0 | 0 | 0 | 0 | 0.001 (0.001) | 0 | 0.001 (0.001) | 0.001 (0.001) |
| *L. berlesei* | ad | 0.012 (0.012) | 0 | 0 | 0 | 0 | 0 | 0.002 (0.002) | 0 | 0.002 (0.002) | 0.003 (0.003) |
| *Cheiroseius borealis* | juv+ad | 0 | 0.001 (0.001) | 0 | 0.008 (0.007) | 0 | + | 0.002 (0.002) | 0.001 (0.001) | 0.002 (0.002) | 0.003 (0.002) |
| *Arctoseius cetratus* | juv+ad | 0.020 (0.013) | 0.004 (0.004) | 0.034 (0.020) | 0.022 (0.016) | 0.002 (0.002) | 0.002 (0.002) | 0.010 (0.005) | 0.026 (0.010) | 0.015 (0.005) | 0.027 (0.008) |
| *A. insularis* | juv | 0 | 0.020 (0.010) | 0.021 (0.019) | 0.008 (0.006) | 0.001 (0.001) | 0.003 (0.003) | 0.007 (0.004) | + | 0.005 (0.003) | 0.008 (0.005) |
| *A. insularis* | ad | 0.020 (0.008) | 0.004 (0.004) | 0.081 (0.029) | 0.081 (0.034) | 0.043 (0.015) | 0.020 (0.009) | 0.034 (0.014) | 0.019 (0.009) | 0.029 (0.010) | 0.050 (0.017) |
| *Mixozercon sellnicki* | juv | 0 | 0.034 (0.022) | 0.003 (0.003) | 0.004 (0.003) | 0 | 0.002 (0.001) | 0.008 (0.007) | 0.004 (0.002) | 0.007 (0.005) | 0.011 (0.008) |
| *M. sellnicki* | ad | 0.025 (0.011) | 0.038 (0.028) | 0.028 (0.013) | 0.019 (0.009) | 0.014 (0.009) | 0.013 (0.012) | 0.022 (0.005) | 0.059 (0.019) | 0.034 (0.007) | 0.060 (0.013) |
| *Rhodacarellus silesiacus* | juv+ad | 0.017 (0.014) | 0.231 (0.084) | 0.089 (0.051) | 0.008 (0.006) | 0.001 (0.001) | 0.002 (0.001) | 0.052 (0.045) | 0.009 (0.004) | 0.038 (0.030) | 0.066 (0.053) |
| *Dendrolaelaps* sp. | ad | 0.016 (0.016) | 0 | 0 | 0 | 0 | 0 | 0.003 (0.003) | 0.001 (0.001) | 0.003 (0.003) | 0.005 (0.004) |
| *Cyrtolaelaps mucronatus* | $N_2$ | 0 | 0 | 0 | 0 | 0.002 (0.002) | 0 | + | 0 | + | + |
| *Holoparasitus excipuliger* | juv | 0 | 0.078 (0.042) | 0.022 (0.022) | 0 | 0 | 0 | 0.016 (0.016) | 0 | 0.010 (0.010) | 0.018 (0.018) |
| *H. excipuliger* | ad | 0.069 (0.048) | 0.015 (0.009) | 0.175 (0.094) | 0.029 (0.014) | 0.037 (0.013) | 0.019 (0.014) | 0.034 (0.010) | 0.020 (0.014) | 0.029 (0.008) | 0.051 (0.014) |
| *Pergamasus brevicornis* | ad | 0.636 (0.260) | 0.091 (0.039) | 0 | 0.371 (0.085) | 0.255 (0.054) | 0.165 (0.024) | 0.303 (0.096) | 0.130 (0.036) | 0.246 (0.065) | 0.431 (0.114) |
| *P. septentrionalis* | ad | 0 | 0.012 (0.012) | 0.228 (0.228) | 0.141 (0.040) | 0.098 (0.028) | 0.031 (0.022) | 0.056 (0.027) | 0.038 (0.012) | 0.050 (0.019) | 0.088 (0.033) |
| *P. brevicornis/septentrionalis* | $N_2$ | 0 | 0.054 (0.026) | 0.232 (0.159) | 0.319 (0.060) | 0.027 (0.011) | 0.014 (0.004) | 0.083 (0.060) | 0.013 (0.004) | 0.059 (0.040) | 0.104 (0.070) |
| *P. misellus* | ad | 0.024 (0.017) | 0.106 (0.046) | 0.158 (0.064) | 0.036 (0.021) | 0.053 (0.022) | 0.027 (0.023) | 0.049 (0.016) | 0.005 (0.004) | 0.034 (0.011) | 0.060 (0.018) |
| *P. lapponicus* coll. | ad | 0.487 (0.214) | 0.144 (0.117) | 0.384 (0.185) | 0.022 (0.022) | 0.272 (0.104) | 0.119 (0.060) | 0.209 (0.081) | 0.041 (0.017) | 0.153 (0.054) | 0.269 (0.095) |
| *P.* spp. | juv | 0.050 (0.041) | 0.222 (0.074) | 0.388 (0.099) | 0.136 (0.046) | 0.107 (0.036) | 0.057 (0.023) | 0.114 (0.032) | 0.016 (0.007) | 0.081 (0.021) | 0.143 (0.037) |
| *Veigaia kochi* | ad | 0 | 0 | 0 | 0.007 (0.007) | 0.020 (0.012) | 0 | 0.006 (0.004) | 0.002 (0.002) | 0.004 (0.003) | 0.008 (0.005) |
| *V. nemorensis* | juv | 0 | 0 | 0 | 0 | 0.012 (0.012) | 0 | 0.002 (0.002) | 0.002 (0.002) | 0.002 (0.002) | 0.004 (0.003) |
| *V. nemorensis* | ad | 0 | 0 | 0 | 0 | 0.014 (0.014) | 0 | 0.003 (0.003) | 0 | 0.002 (0.002) | 0.003 (0.003) |
| *V. cerva* | juv | 0 | 0 | 0 | 0 | 0.002 (0.002) | 0 | 0.001 (0.001) | 0 | + | 0.001 (0.001) |
| *V. cerva* | ad | 0 | 0 | 0 | 0 | 0.022 (0.016) | 0.012 (0.012) | 0.007 (0.005) | 0 | 0.005 (0.003) | 0.008 (0.005) |
| Gamasina sp. | juv | 0.019 (0.010) | 0.112 (0.029) | 0.111 (0.041) | 0.035 (0.026) | 0 | 0.007 (0.007) | 0.035 (0.021) | 0 | 0.023 (0.014) | 0.041 (0.024) |
| Gamasina, total | | 1.431 | 1.184 | 2.002 | 1.275 | 0.981 | 0.496 | 1.073 (0.162) | 0.392 (0.039) | 0.846 (0.109) | 1.487 (0.191) |
| *Dinychus* sp. | juv | 0.011 (0.008) | 0.001 (0.001) | 0.055 (0.026) | 0.012 (0.008) | 0.003 (0.003) | 0.003 (0.003) | 0.006 (0.003) | 0.001 (0.001) | 0.004 (0.002) | 0.007 (0.003) |
| *D.* sp. | ad | 0.013 (0.013) | 0 | 0 | 0.020 (0.013) | 0.018 (0.012) | 0.006 (0.005) | 0.011 (0.004) | 0.005 (0.003) | 0.009 (0.003) | 0.016 (0.005) |
| Uropodina sp. | juv+ad | 0 | 0.001 (0.001) | 0 | 0.002 (0.002) | 0 | 0 | 0.001 (0.001) | 0.001 (0.001) | 0.001 (0.001) | 0.001 (0.001) |
| Uropodina, total | | 0.024 | 0.002 | 0.055 | 0.033 | 0.021 | 0.009 | 0.018 (0.006) | 0.007 (0.003) | 0.014 (0.004) | 0.025 (0.007) |

Table 50. Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) and annual respiration (kcal $m^{-2}$) of Prostigmata and Astigmata in 1971–72. The August values are not used for calculating "summer" and annual means. Standard error is given within parentheses below the corresponding mean value. + denotes a value less than 0.0005.

| | | Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) | | | | | | | | | Annual respiration (kcal $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | May 17 | June 15 | Aug 4 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual | |
| Pyemotidae spp. | juv+ad | 0.014 (0.004) | 0.010 (0.003) | 0.033 (0.019) | 0.027 (0.011) | 0.025 (0.019) | 0.023 (0.007) | 0.020 (0.004) | 0.015 (0.005) | 0.018 (0.003) | 0.032 (0.005) |
| *Scutacarus* spp. | juv+ad | 0.033 (0.014) | 0.014 (0.005) | 0.021 (0.008) | 0.008 (0.003) | 0.009 (0.003) | 0.004 (0.003) | 0.014 (0.006) | 0.008 (0.002) | 0.012 (0.004) | 0.020 (0.007) |
| Tarsonemidae sp. | juv+ad | 0.005 (0.002) | 0.010 (0.004) | 0.025 (0.010) | 0.022 (0.006) | 0.017 (0.004) | 0.016 (0.004) | 0.014 (0.003) | 0.004 (0.001) | 0.011 (0.002) | 0.019 (0.004) |
| Eriophyidae sp. | juv+ad | 0 | 0.001 (0.001) | 0.003 (0.002) | 0.001 (0.001) | 0 | 0.005 (0.004) | 0.002 (0.001) | 0.001 (0.001) | 0.001 (0.001) | 0.002 (0.002) |
| Anystidae sp. | ad | 0 | 0 | 0 | 0.034 (0.019) | 0 | 0 | 0.007 (0.007) | 0 | 0.005 (0.003) | 0.008 (0.005) |
| Prostigmata spp. | juv+ad | 0.215 (0.038) | 0.323 (0.043) | 1.139 (0.336) | 0.133 (0.022) | 0.086 (0.015) | 0.161 (0.048) | 0.184 (0.041) | 0.280 (0.049) | 0.216 (0.032) | 0.380 (0.056) |
| Prostigmata, total | | 0.268 | 0.358 | 1.220 | 0.225 | 0.136 | 0.210 | 0.239 (0.037) | 0.308 (0.051) | 0.262 (0.030) | 0.460 (0.052) |
| *Histiostoma* cf. *feroniarum* | juv+ad | 0.012 (0.005) | 0.015 (0.007) | 0.075 (0.031) | 0.046 (0.014) | 0.009 (0.004) | 0.012 (0.004) | 0.019 (0.007) | 0.010 (0.003) | 0.016 (0.005) | 0.028 (0.008) |
| *Schwiebea cavernicola* | juv+ad | 0.048 (0.030) | 0.147 (0.108) | 1.439 (0.676) | 0.094 (0.031) | 0.337 (0.100) | 0.084 (0.043) | 0.142 (0.052) | 0.159 (0.044) | 0.147 (0.038) | 0.259 (0.066) |
| Astigmata sp. | juv | 0 | 0.002 (0.002) | 0 | 0 | 0 | 0 | + | + | + | 0.001 (0.001) |
| Astigmata, total | | 0.060 | 0.164 | 1.513 | 0.139 | 0.346 | 0.096 | 0.161 (0.050) | 0.169 (0.045) | 0.164 (0.037) | 0.288 (0.064) |

and Astigmata. The annual respiration of Prostigmata was estimated at 0.46 (*s.e.* = 0.06) kcal $m^{-2}$ and that of Astigmata at 0.29 (*s.e.* = 0.07) kcal $m^{-2}$. The dominant astigmatid *Schwiebea cavernicola* accounted for 0.26 (*s.e.* = 0.07) kcal $m^{-2}$ $yr^{-1}$.

The oxygen consumption rates and annual respiration of different oribatids and total Acari are presented in Table 51. *Tectocepheus sarekensis* had the highest annual respiration of the oribatids with 0.25 kcal $m^{-2}$. Other species with relatively high annual respiration were *Oppia* spp., Brachychthoniidae spp. and *Trichoribates trimaculatus* with 0.14, 0.14 and 0.12 kcal $m^{-2}$, respectively. The annual respiration of total Cryptostigmata was estimated at 0.68 (*s.e.* = 0.09) kcal $m^{-2}$.

The oxygen consumption rates of total Acari ranged from about 1 $cm^3$ $O_2$ $m^{-2}$ $day^{-1}$ at the November sampling to almost 6 $cm^3$ $O_2$ $m^{-2}$ $day^{-1}$ at the supplementary August sampling. The great differences were mainly caused by the high temperature dependence. The annual respiration of total Acari was estimated at 2.9 (*s.e.* = 0.28) kcal $m^{-2}$, of which Mesostigmata, Prostigmata, Astigmata and Cryptostigmata contributed 1.5, 0.5, 0.3 and 0.7 kcal $m^{-2}$, respectively.

Table 51. Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) and annual respiration (kcal $m^{-2}$) of Cryptostigmata and total Acari in 1971–72. The August values are not used for calculating "summer" and annual means. Standard error is given within parentheses below the corresponding mean value. + denotes a value less than 0.0005.

| | | Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) | | | | | | | | | Annual respiration (kcal $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | May 17 | June 15 | Aug 4 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual | |
| *Steganacarus striculus* | ad | 0 | 0 | 0.006 (0.006) | + | 0 | 0 | + | 0 | + | + |
| *Hypochthonius rufulus* | ad | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.001 (0.001) | + | 0.001 (0.001) |
| Brachychthoniidae spp. | juv | 0.006 (0.001) | 0.050 (0.022) | 0.204 (0.050) | 0.051 (0.014) | 0.014 (0.004) | 0.014 (0.004) | 0.027 (0.010) | 0.010 (0.002) | 0.021 (0.007) | 0.037 (0.012) |
| B. spp. | ad | 0.058 (0.015) | 0.050 (0.016) | 0.024 (0.008) | 0.130 (0.025) | 0.067 (0.017) | 0.042 (0.010) | 0.069 (0.016) | 0.044 (0.009) | 0.061 (0.011) | 0.107 (0.020) |
| *Platynothrus peltifer* | juv | 0 | 0 | 0 | 0 | 0 | 0.001 (0.001) | + | 0.001 (0.001) | + | + |
| *P. peltifer* | ad | 0 | 0 | 0 | 0 | 0 | 0 | 0 | + | + | + |
| *Damaeus clavipes* | ad | 0 | 0 | 0 | 0 | 0 | 0.001 (0.001) | + | 0 | + | + |
| *D. verticillipes* | juv | 0 | 0 | 0 | 0 | 0.001 (0.001) | 0.006 (0.006) | 0.001 (0.001) | 0 | 0.001 (0.001) | 0.002 (0.002) |
| *D. verticillipes* | ad | 0 | 0 | 0.036 (0.036) | 0 | 0.001 (0.001) | 0.004 (0.004) | 0.001 (0.001) | 0 | 0.001 (0.001) | 0.001 (0.001) |
| *Carabodes areolatus* | ad | 0 | 0 | 0 | 0.005 (0.005) | 0 | 0 | 0.001 (0.001) | 0 | 0.001 (0.001) | 0.001 (0.001) |
| *Tectocepheus sarekensis* | juv | 0.075 (0.017) | 0.075 (0.029) | 0.181 (0.055) | 0.105 (0.025) | 0.064 (0.015) | 0.031 (0.008) | 0.070 (0.012) | 0.027 (0.004) | 0.056 (0.008) | 0.098 (0.014) |
| *T. sarekensis* | ad | 0.145 (0.038) | 0.196 (0.056) | 0.338 (0.058) | 0.119 (0.023) | 0.069 (0.018) | 0.038 (0.014) | 0.114 (0.028) | 0.040 (0.008) | 0.089 (0.019) | 0.156 (0.033) |
| *Oppia minus/nova* | juv | 0.002 (0.001) | 0 | 0.009 (0.003) | 0.001 (0.001) | 0.001 (0.001) | 0.004 (0.002) | 0.002 (0.001) | 0.009 (0.004) | 0.004 (0.002) | 0.007 (0.003) |
| *O. minus/nova* | ad | 0.051 (0.008) | 0.218 (0.055) | 0.095 (0.028) | 0.018 (0.006) | 0.024 (0.006) | 0.045 (0.019) | 0.071 (0.037) | 0.093 (0.020) | 0.078 (0.026) | 0.138 (0.046) |
| *Suctobelba subtrigona* | ad | 0 | 0 | 0 | 0 | 0.002 (0.002) | 0 | + | 0 | + | + |
| *Oribatula tibialis* | ad | 0 | 0 | 0 | 0 | 0 | 0.002 (0.002) | + | 0 | + | 0.001 (0.001) |
| *Hemileius initialis* | ad | 0 | 0 | 0 | 0 | 0.004 (0.004) | 0 | 0.001 (0.001) | 0.005 (0.003) | 0.002 (0.001) | 0.004 (0.002) |
| *Scheloribates laevigatus* | ad | 0 | 0 | 0.018 (0.018) | 0 | 0 | 0 | 0 | 0.004 (0.004) | 0.001 (0.001) | 0.002 (0.002) |
| *Chamobates cuspidatus* | ad | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.004 (0.002) | 0.001 (0.001) | 0.002 (0.002) |
| *Trichoribates trimaculatus* | juv | 0.007 (0.007) | 0.010 (0.005) | 0.034 (0.025) | 0.014 (0.005) | 0.084 (0.038) | 0.037 (0.009) | 0.030 (0.015) | 0.056 (0.012) | 0.039 (0.011) | 0.068 (0.019) |
| *T. trimaculatus* | ad | 0.018 (0.018) | 0.051 (0.020) | 0.059 (0.059) | 0.048 (0.017) | 0.041 (0.014) | 0.012 (0.003) | 0.034 (0.008) | 0.015 (0.003) | 0.028 (0.006) | 0.048 (0.010) |
| *Neoribates aurantiacus* | ad | 0 | 0 | 0 | 0.010 (0.005) | 0.019 (0.015) | 0.005 (0.004) | 0.007 (0.004) | 0.001 (0.001) | 0.005 (0.003) | 0.008 (0.005) |
| Cryptostigmata sp. | juv | 0 | 0.007 (0.004) | 0.004 (0.004) | 0 | 0 | 0 | 0.001 (0.001) | + | 0.001 (0.001) | 0.002 (0.002) |
| Cryptostigmata, total | | 0.361 | 0.658 | 1.006 | 0.501 | 0.390 | 0.243 | 0.430 (0.071) | 0.308 (0.022) | 0.390 (0.048) | 0.684 (0.084) |
| Acari, total | | 2.144 | 2.365 | 5.795 | 2.173 | 1.874 | 1.053 | 1.922 (0.231) | 1.184 (0.081) | 1.676 (0.157) | 2.944 (0.275) |

## Discussion

### Vertical distribution

Seasonal variations in vertical distribution of Acari have been observed by many investigators, e.g. van der Drift (1951), Strenzke (1952), Karppinen (1955, 1958), Stöckli (1957), Wallwork (1959), Tarras-Wahlberg (1961) and Usher (1971), and most of the changes seem to be caused by vertical migration. The migration is generally initiated by drought or low temperatures in the upper layers of the soil, and especially in northern countries the temperature factor is obviously very important for downward migration (Karppinen, 1955, 1958; Tarras-Wahlberg, *op. cit.*; Usher, *op. cit.*). Cold was apparently more important than drought for causing vertical migration at Spikbole during the study period. The seasonal changes of vertical distribution of Acari were very alike those of Collembola, and in both groups the changes were chiefly assigned to small and slender forms which were able to use the small soil interstices at greater depths. However, the numbers of soil-inhabiting mites were probably underestimated during the "summer" period due to inefficient extraction (see below) and thus there is a possibility that the unextracted mites had a different vertical distribution than the extracted ones. This "selective extraction" complicates the understanding of the occurrence of animals in the vertical profile.

### Abundance

Winter maxima of soil mites have been reported by many authors working in localities with relatively mild winter climate, e.g. Macfadyen (1952) and Evans (1955) in England, and Strenzke (1952) in Germany, but winter maxima have also been recorded in areas with harder winter climate (Huhta *et al.*, 1967). The highest abundances of Prostigmata, Cryptostigmata, some Gamasina species and total Acari at Spikbole were also estimated during the "winter", but other indications contradicted the occurrence of peak numbers in the "winter". The marked increase in numbers of Prostigmata and Cryptostigmata from October to the "winter" should have coincided with a great increase in juveniles, but actually the proportion of juvenile Cryptostigmata (juvenile Prostigmata were not separated from adults) decreased successively during this period. The low soil temperatures from November onwards would have largely prevented hatching, and consequently the mortality rate should have balanced or even exceeded the natality rate, resulting in equal or lower abundances during the "winter" than during the late autumn. Therefore, the high abundances obtained during the "winter" were probably caused by more efficient extraction due to the maintenance of the structure in the frozen soil cores, as already discussed for Collembola (p. 76).

A summer peak density was, nevertheless, estimated for total Gamasina, which also consisted of soil-dwelling forms, and this maximum was correlated with a high proportion of juveniles. *Arctoseius insularis* and *Mixozercon sellnicki* obtained peak numbers of juveniles in June. The development of these small gamasids was relatively rapid, since the proportion of adults had increased and exceeded that of juveniles already in August. The results are somewhat obscured by the inefficient extraction during the "summer", but there is no evidence of a second generation. The real peak abundance probably occurred during the summer at the same time as the juvenile peak. Population maxima during the summer have been recorded for *Arctoseius bispinatus* Weis-Fogh (= *A. cetratus*)

in an English grassland (Dhillon & Gibson, 1962) and for Zerconidae in Bavarian coniferous forests (Elbadry, 1973).

The data on the larger *Pergamasus* species, *P. brevicornis, P. septentrionalis* and *P. lapponicus*, are not unanimous, especially since the juveniles were not separated into species, but suggest that there was primarily a summer hatching period, after which the juvenile development lasted for several months. The adult stage was probably not reached until the late autumn or even the early spring, after which the adults dominated in May. Adults found during the summer probably belonged to the preceding year's generation. This is in agreement with the rearing experiments made by Bhattacharyya (1962), who found that the mean rate of development of *Pergamasus crassipes* (L.) from the larval to the adult stage was 46 days at +15°C and 82 days at +7.3°C. The average longevity of the adult stage was 102 days for males and 125 days for females at +15°C (Bhattacharyya, *op. cit.*), thus indicating a total longevity of more than a year at the temperatures found at Spikbole. However, Bhattacharyya (*op. cit.*) could not find any marked seasonal variations in the population density in a woodland habitat in South Wales. Usher (1971) recorded autumn peak abundances of adult *Pergamasus lapponicus* in a pine forest soil in Scotland, which might indicate a similar type of development as at Spikbole, but did not find any obvious seasonal trend for the population size of juvenile Mesostigmata. Seasonal variations of Parasitidae have also been reported by other authors. Van der Drift (1951) recorded population maxima of Parasitidae, mainly *Pergamasus* and *Veigaia*, in October in a Dutch beech forest. Dhillon & Gibson (1962) found summer maxima and winter minima of Parasitidae in an English grassland, and Elbadry (1973) obtained July and December maxima for Parasitidae in two Bavarian coniferous forest soils.

A peak abundance of *Rhodacarellus silesiacus* was estimated at the June sampling, but since adults and juveniles were not separated on that occasion there are no age class data to support the assumption of an early summer hatching for this species. Karg (1961) observed a summer density maximum of *R. silesiacus* in a potato field in Germany, where the maximum was correlated with the occurrence of larvae and nymphs. On the other hand, he found winter and spring maxima in a grass field in the same area, which he interpreted as an effect of the higher soil temperatures during the winter due to the insulating vegetation and litter layer. Karg (*op. cit.*) recorded summer maxima of total Gamasina in both fields, and the maxima were always correlated with a higher number of larvae, nymphs and gravid females. He also observed that the development from larvae to adults mainly occurred from May to October, i.e. the development started somewhat earlier than at Spikbole. Luxton (1967) estimated a distinct rise in numbers of total Mesostigmata in August in a Welsh saltmarsh, but there was little evidence of seasonal variation in numbers of juvenile Mesostigmata.

Thus, there are many reports on summer peak densities of Gamasina species, total Gamasina and total Mesostigmata, and there is also evidence of summer hatching in many areas. However, hatching is not necessarily restricted to the summer in areas with mild winter climate, and therefore peak numbers may occur at other seasons (Karg, 1961; McMillan, 1969). At Spikbole, however, the hatching seems to be restricted to the summer for most Gamasina species.

Brachychthoniidae spp. was the only oribatid group that showed a distinct summer density peak correlated with the occurrence of many juveniles. The two species

*Brachychochthonius immaculatus* and *Liochthonius sellnicki* seemed to have a parallel development, but it was not clear whether they had one or more generations a year. Van der Drift (1951) found a distinct maximum of Brachychthoniidae in the early summer in a Dutch beech forest, thus indicating a slightly earlier hatching than at Spikbole.

The number of juvenile *Tectocepheus sarekensis* did not change significantly over the year, although the juvenile/adult ratio was highest during the autumn months. Haarløv (1960) obtained a larval density maximum of *T. velatus* (Mich.) in a Danish soil during July–September and found it possible for *T. velatus* to develop two generations a year. Murphy & Jalil (1964) also found support for two generations a year for both *T. velatus* and *T. sarekensis* in an English soil. They estimated the duration of the egg and juvenile stages at 102 days for these species when cultured in the laboratory at +25°C. The corresponding development time for the juveniles was 89 days. Thus, assuming $Q_{10} = 2$ and hatching in August, this implies that the juvenile stages would last about 11 months under the temperature conditions at Spikbole. Consequently, only one generation a year would be probable for *T. sarekensis* at Spikbole.

Relatively few juvenile *Oppia* spp. were recorded during the "summer" period. This might have been caused by inefficient extraction due to compression of the soil cores, but could also reflect the short duration of the juvenile stages. Woodring & Cook (1962) estimated the development time of *Oppia nova* at 23 days from egg to adult at +25°C, which may allow two or more generations a year even at the temperatures occurring at Spikbole.

The species discussed here are only part of the total acarine fauna at Spikbole, and the fluctuations of total Acari are dependent on the variations of each individual species, although primarily the most abundant ones. Generally the hatching periods seemed to occur during the summer and early autumn, and no indications of hatching were observed during the late autumn, winter and spring. A tentative conclusion is that most species appeared to have one generation a year and only smaller species seemed to have more than one generation a year.

The annual mean abundance of total Acari at Spikbole, about 110 000 specimens $m^{-2}$, is similar to density data obtained in other temperate grassland localities. Annual or summer means of 70 000–180 000 $m^{-2}$ have been recorded by Macfadyen (1952), Hairston & Byers (1954), Haarlov (1960), Block (1965), Wood (1967), Curry (1969), McMillan (1969), Adams (1971), Lebrun (1971) and Östbye *et al.* (1975) in a variety of grassland sites. Mean densities lower than 70 000 $m^{-2}$ of total Acari are also frequently reported from grassland soils, but values lower than 20 000 $m^{-2}$ mostly indicate an extreme climatic condition or inefficient extraction methods. Peak values higher than 180 000 $m^{-2}$ are often reported in different grasslands, and McMillan (1969) found a maximum of 580 000–590 000 mites $m^{-2}$ in a New Zealand grassland. Even higher abundances have been recorded in coniferous forest soils (Forsslund, 1943; Persson, 1975).

Cryptostigmata is generally considered as the dominant mite group in most soils (Macfadyen, 1952; Evans *et al.*, 1961; Block, 1965; Lebrun, 1971), but the higher abundances of Prostigmata at Spikbole are by no means exceptional, and several investigators have found higher densities of Prostigmata than of Cryptostigmata in grassland localities (Dhillon & Gibson, 1962; Loots & Ryke, 1966, 1967; Karg, 1967; Wood, 1967). The

abundances of Mesostigmata fell within the range 4000–15 000 $m^{-2}$, which is often recorded in grasslands (Macfadyen, 1952; Dhillon & Gibson, 1962; Block, 1965; McMillan, 1969), but also higher densities have been reported by, for example, Salt *et al.* (1948), Haarløv (1960), Wood (1967), Curry (1969) and Lebrun (1971). The dominance of Gamasina over Uropodina contrasts with the results obtained by Lebrun (1971), who found more Uropodina than Gamasina specimens in a Belgian grassland. The number of Astigmata at Spikbole ranged from 2500 to 36 000 $m^{-2}$ with an annual mean of about 15 000 $m^{-2}$. This seems to be fairly high in comparison with most other data, although higher numbers have been recorded in a Swedish pine forest, where Persson (1975) found about 60 000 astigmatids $m^{-2}$.

Dissimilarities from year to year in mite abundances have been observed by, for example, Karg (1961), Block (1966a) and Huhta *et al.* (1967). The only results at Spikbole outside the main study period 1971 -72 are those obtained in May 1970 (Appendix 1). The abundances of Mesostigmata and total Acari were relatively low on that occasion, and thus in agreement with the results in May 1971.

**Biomass**

The annual mean biomass of total Acari of 130 mg dw $m^{-2}$ is fairly low compared with most other grassland soils. Estimates of a similar order are reported by Bunnell *et al.* (1975), who found 110 mg dw $m^{-2}$ in an Alaskan meadow, and by Crossley *et al.* (1975), who obtained biomasses around 170–180 mg dw $m^{-2}$ during May -August in ungrazed grassland sites in Colorado. Engelmann (1961), using the data from Hairstone & Byers (1954), calculated the biomass to be about 55 mg dw $m^{-2}$ in an abandoned field in Michigan. Most of the biomass estimates reported in the literature are however higher. Chernov *et al.* (1975) reported an acarine biomass of 500 mg fw $m^{-2}$, i.e. 200 mg dw $m^{-2}$ assuming a dry weight content of 40 %, in herb-grass stands in Western Taimyr. Østbye *et al.* (1975) found mean biomasses of about 200–600 mg dw $m^{-2}$ in two alpine meadows in Norway. Block (1966a) estimated the annual mean biomass of Acari at 890 1850 mg fw $m^{-2}$, i.e. 360–740 mg dw $m^{-2}$, in high-altitude grasslands in England. Even higher values are given by Lebrun (1971), who obtained an annual mean of 3880 mg fw $m^{-2}$, i.e. 1550 mg dw $m^{-2}$, in a grass field in Belgium. The biomass of single groups of Acari have been estimated by, for example, Macfadyen (1952) who reported 200 1400 mg fw $m^{-2}$ for Cryptostigmata in a *Molinia* fen in England.

The higher biomasses obtained in many localities could generally be assigned to higher mean body weights than at Spikbole. The mean body weights of Meso- and Cryptostigmata were, for example, 100 and 13 μg fw, respectively, in an English *Nardus stricta* grassland (Block, 1965, 1966a), while the corresponding mean weights at Spikbole were 22 and 2.5 μg fw, i.e. about five times lower. Lebrun (1971) obtained a mean weight of about 30 μg fw for Cryptostigmata in a Belgian grassland, the mean weight at Spikbole being 12 times lower. Only Engelmann (1961) reported a mean weight of Cryptostigmata similar to that at Spikbole. Many investigators have used different methods of calculating mean body weights of Acari, which naturally leads to differing results. The main differences in mean body weights were probably caused by the dominance of smaller forms at Spikbole than at most other localities, but it is also possible that the extraction method used at Spikbole was more efficient than most other methods with regard to the extraction of juveniles.

**Respiration**

Published data on the respiratory rates of soil mites have chiefly concerned adult individuals, but Webb (1969) and Wood & Lawton (1973) estimated the respiratory rates of the juvenile stages of some Mesostigmata and Cryptostigmata species. The data indicate that the weight specific respiratory rates of juvenile Acari differ from that of the adults, but Wood & Lawton (*op. cit.*) suggest that for some purposes "regressions based on data obtained for adult mites only, could provide a reasonable estimate of the respiratory rates of juvenile stages of a similar live weight, within the same taxonomic group". Few determinations have been made on respiratory rates of very small mites, and in order to calculate the rates of mites smaller than 1–2 μg the regressions used in this study have been extrapolated outside their validity range. Another approximation used here is the assumption of a mean oxygen consumption rate for adults of a species. Actually there are differences between males and females and between gravid and non-gravid females (Wood & Lawton, *op. cit.*), which complicate the respiration calculations.

The annual respiration of about 3 kcal $m^{-2}$ $yr^{-1}$ for the total Acari is fairly low owing to the relatively low biomass and the low soil temperature. The presumed underestimation of the soil-inhabiting species during the "summer" probably affected the respiration estimates considerably, but the annual respiration should hardly have exceeded 5 kcal $m^{-2}$ $yr^{-1}$. Engelmann (1961), using the population data from Hairston & Byers (1954), calculated the annual respiration to be only 1.1 kcal $m^{-2}$ $yr^{-1}$ for the Acari populations in an abandoned field in Michigan. Most other data on the respiration of Acari are equal to or higher than that at Spikbole. Dunger (1968) recorded the annual respiration to be 0.9–4.2 kcal $m^{-2}$ $yr^{-1}$ in early succession stages on brown coal dumps in Germany, and Huhta & Koskenniemi (1975) reported respiration figures of 3.0–9.2 kcal $m^{-2}$ $yr^{-1}$ in Finnish spruce stands. In a detailed study Berthet (1964) estimated the annual respiration of adult Cryptostigmata at 21.5 kcal $m^{-2}$ $yr^{-1}$ in a Belgian oak forest. He suggested that the oribatids would respire about 2–3 times as much when the juveniles were included, and consequently an annual value of about 50 kcal $m^{-2}$ $yr^{-1}$ could be expected for total Cryptostigmata. Berthet (1967) reported respiration figures for adult oribatids to be 2.4–8.9 kcal $m^{-2}$ $yr^{-1}$ in the litter layers of different forests, which he assumed to be equivalent to about 30 kcal $m^{-2}$ $yr^{-1}$ for all oribatids in the whole soil profile. High estimates have also been reported from grassland soils, where Macfadyen (1963) reported an annual respiration of 8.3 kcal $m^{-2}$ $yr^{-1}$ for Oribatei in an upland limestone grassland in England and 10.2 kcal $m^{-2}$ $yr^{-1}$ for Oribatei and 63.6 kcal $m^{-2}$ $yr^{-1}$ for Parasitidae in an English grazed meadow. The latter value is probably an overestimation, since the respiration rate for a parasitid of 100 μg live body weight is about four times higher than that found by Wood & Lawton (1973). Respiratory rates similar to those given by Wood & Lawton (*op. cit.*) were determined by Webb (1970a), who estimated the total annual respiration of *Rhodacarus roseus* Oudms, *Pachylaelaps lindrothi* Sell., *Eviphis ostrinus* C.L.K. and *Trachytes pyriformis* (Kramer) at 0.09 0.15 kcal $m^{-2}$ at three sites in a Danish *Calluna* heath area. The annual respiration of the oribatid *Nothrus silvestris* Nic. was estimated at 0.57 kcal $m^{-2}$ in the same area (Webb, 1970b).

**Feeding habits**

The feeding habits of Acari are extremely diverse and the main feeding categories herbivores, saprovores, microbivores and carnivores have many representatives within this taxon. The gamasids are generally considered as predatory mites with more or less specialized feeding habits. Karg (1961, 1971) has found striking relationships between the life forms of the gamasids and their prey animals. The large-sized, surface-living *Pergamasus* species feed on larger Collembola, weakly sclerotized Acari, insect larvae and Enchytraeidae. *Veigaia nemorensis* seems to be specialized on Collembola, e.g. *Folsomia quadrioculata*, while the *Hypoaspis* species are more polyphagous. The small soil-inhabiting gamasids prefer Nematoda, Collembola and soft-bodied Acari, and *Rhodacarellus silesiacus*, for example, often feed on Nematoda and small Collembola like *Tullbergia krausbaueri* (Karg, *op. cit.*). The Zerconidae may be predators, although more information is needed on their feeding habits (Wallwork, 1967). Members of the Uropodina are mainly fungivorous and coprophagous (Wallwork, 1970), but may also be algivorous, since *Dinychus perforatus* (Kramer), for example, survived better in culture with *Pleurococcus* than when provided with other foods (Bhattacharyya, 1962).

Several forms of Prostigmata, such as Bdellidae, Cunaxidae, Rhagidiidae, Anystidae and Erythraeidae, are known to be predatory. Tydeidae have been considered as predacious by some authors and fungivorous by others (Wallwork, 1967). Very little is known about the feeding of many other soil Prostigmata groups, e.g. Pyemotidae, Scutacaridae and Tarsonemidae (Wallwork, 1970). Some of the above-ground Pyemotidae and Tarsonemidae contain important herbivorous species (Evans *et al.*, 1961), of which *Siteroptes* sp. was also found in the soil samples from Spikbole. Other plant-feeding prostigmatids observed in the soil samples were Eriophyidae and Tetranychidae.

The feeding habits of soil-dwelling Astigmata are not well known. *Schwiebea talpa* Oudms probably feeds on fungi and products of fungal decay in certain situations (Wallwork, 1967). The anoetids are basically filter feeders on liquids rich in bacteria, yeasts and unicellular fungi (Woodring, 1963).

Considerable knowledge has been accumulated on the feeding habits of soil Cryptostigmata, which are reviewed by Berthet (1964), Wallwork (1967, 1970), Lebrun (1971), Luxton (1972) and Harding & Stuttard (1974). Relatively few species, mainly belonging to Euphthiracaridae and Phthiracaridae, are strictly "macrophytophages" and feed on decaying parts of higher plants (Luxton, 1972). Other oribatids are specialized on microorganisms, "microphytophages", of which most are fungivorous, e.g. Damaeidae, Oppioidea and possibly Eremaeoidea, while *Hypochthonius rufulus* C.L.K. appears to have a predilection for bacteria (Luxton, *op. cit.*). The large majority of Cryptostigmata are, however, unspecialized feeders on both microbial growths and dead plant material. A few Cryptostigmata species, such as *Scheloribates laevigatus* (C.L.K.), have been observed to feed on living prey, and other species e.g. *Hemileius initialis* (Berl.) and *Liochthonius* sp. have been found feeding on carrion, but this is probably only a supplement to the more usual diet of decaying organic material (Wallwork, 1970). Some Cryptostigmata are also coprophagous, and faecal-feeding may be common among immature stages of phthiracarids that burrow in woody tissue (Wallwork, 1970).

. Following the terminology in Fig. 1, all Uropodina, Astigmata and Cryptostigmata at Spikbole were classified as saprovores/microbivores, and Gamasina as below-ground carnivores. The Prostigmata group consisted of several feeding categories, but it is reasonable to

assume that about 50 % were below-ground carnivores, 40 % were saprovores/microbivores and 10 % were above-ground herbivores. This proportion was assumed for abundance and biomass as well as for respiration.

## OTHER TAXA

### Introduction

The soil fauna samples from Spikbole included arthropod groups with members occurring at very low abundances and/or biomasses. These groups were Isopoda, Symphyla, Protura, Diplura, Blattodea, Psocoptera, Homoptera and Opiliones, and although taxonomically very different, these arthropods have been treated together in this chapter.

### Methods

The different extraction methods used are indicated in Table 52. The weight determinations of Isopoda, Symphyla, Blattodea and Opiliones were based on individual weighings, while specimens of Cicadina (Homoptera) were weighed collectively owing to their small sizes. The body weights of Protura, Diplura and Psocoptera were derived from measurements of body length. The relationship between live body weight in $\mu$g ($W$) and body length in mm ($L$) was calculated as $W = (1.16 \cdot L)^3$ for Diplura and $W = (1.64 \cdot L)^3$ for Psocoptera (Edwards, 1967). The corresponding equation for Protura was assumed to be $W = (1.20 \cdot L)^3$ in analogy with animals of similar body shape. The mean live body weights of Protura, Pscocoptera and Diplura were used for calculating the biomass and respiratory rates and were 1.0, 2.2 and 19 $\mu$g, respectively. The dry weight/live weight ratios used were 0.27 for Isopoda (Edwards, *op. cit.*), 0.17 for Symphyla (Edwards, *op. cit.*), 0.305 for Diplura (Edwards, *op. cit.*) and 0.25 for Protura, Blattodea, Psocoptera, Homoptera and Opiliones (assumptions).

The oxygen consumption rate of Isopoda was calculated from Reichle's (1968) data on *Metoponorthus pruinosus* (Brandt) corrected to the actual body weight assuming that the oxygen consumption rate was proportional to the 0.84 power of the live body weight (cf. Reichle, *op. cit.*). The corresponding equation was $Q = 176.1 \cdot W^{0.84}$, where $Q$ denotes $mm^3$ $O_2$ $ind^{-1}$ $h^{-1}$ at +20°C and $W$ denotes g live body weight. The oxygen consumption rate at +20°C was adjusted to the field temperature by assuming a $Q_{10} = 2$ down to +5°C, below which the rate was assumed to decline linearly with temperature to a zero-value at −5°C (cf. Enchytraeidae).

The oxygen consumption rates of Symphyla, Protura, Diplura, Psocoptera and Coccina were calculated according to the equation and temperature correction factors given for Collembola, i.e. $Q = 63 \cdot W^{0.73}$ at +18°C and $Q_{10} = 2.6$ down to +5°C and $Q_{10} = 3.6$ below +5°C (cf. Collembola). For each of these taxa the mean live body weight was used in the equations.

The relationship between oxygen consumption rate and ash free dry body weight of *Blattella germanica* L. has been presented by Woodland *et al.* (1968). The equation for

younger *B. germanica* was $Q = 256 \cdot W^{0.702}$ at +28°C when given in a form similar to that of *M. pruinosus*, i.e. where $W$ was g live body weight. The equation was used for calculating the oxygen consumption rates of *Ectobius lapponicus* L. The rates were adjusted to the field temperature by assuming $Q_{10} = 2$ down to +5°C and $Q_{10} = 4$ below +5°C.

The oxygen consumption rates of Opiliones were calculated according to Phillipson's (1963) regression line (Fig. 2) on *Leiobunum rotundum* (Latr.) which corresponds to an equation of $Q = 381 \cdot W^{0.79}$ at +16°C. The $Q_{10}$ was assumed to be 2 down to +10°C.

## Results

The species composition, abundance, biomass and respiration of the taxa considered in this chapter are shown in Tables 52–54. The estimates are generally based on few individuals and the standard errors are therefore relatively high, indicating a low degree of precision. Coccina sp. (Homoptera) and *Eosentomon* cf. *germanicum* Prell (Protura) had the highest abundances (Table 52), while Porcellionidae sp. (Isopoda) and *Ectobius lapponicus* (Blattodea) had the highest biomasses (Table 53). *E. lapponicus* had the greatest contribution to the annual respiration (Table 54).

**Table 52.** **Abundance (no. $m^{-2}$) of litter- and soil-inhabiting Isopoda, Symphyla, Protura, Diplura, Blattodea, Psocoptera, Homoptera and Opiliones in 1971–72. The August values are not used for calculating "summer" and annual means. Standard error is given within parentheses below the corresponding mean value.**
**n.e. = not estimated**
**M = Macfadyen high gradient canister extraction**
**T = Tullgren funnel extraction**
**H = Hand sorting**

| | | May 17 | June 15 | Aug 4 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|---|
| **Isopoda** | | | | | | | | | | |
| Porcellionidae sp. | (H) | 0 | 0 | n.e. | 0 | 0 | 0 | 0 | 1.3 (1.3) | 0.4 (0.4) |
| **Symphyla** | | | | | | | | | | |
| *Scutigerella* cf. *immaculata* | (H) | 0 | 0 | n.e. | 0 | 0 | 1.1 (1.1) | 0.2 (0.2) | 0 | 0.1 (0.1) |
| **Protura** | | | | | | | | | | |
| *Eosentomon* cf. *germanicum* | (M) | 0 | 123.5 (123.5) | 61.7 (61.7) | 61.7 (61.7) | 123.5 (84.1) | 0 | 61.7 (27.6) | 0 | 41.2 (18.4) |
| **Diplura** | | | | | | | | | | |
| *Campodea* sp. | (M) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 74.1 (74.1) | 24.7 (24.7) |
| **Blattodea** | | | | | | | | | | |
| *Ectobius lapponicus* | (H) | 0 | 0 | n.e. | 2.1 (1.5) | 4.3 (2.9) | 0 | 1.3 (0.9) | 0.5 (0.5) | 1.0 (0.6) |
| **Psocoptera** | | | | | | | | | | |
| Psocoptera sp. | (M) | 61.7 (61.7) | 61.7 (61.7) | 61.7 (61.7) | 123.5 (84.2) | 0 | 0 | 49.4 (23.1) | 0 | 32.9 (15.4) |
| **Homoptera** | | | | | | | | | | |
| Coccina sp. | (M+T) | 0 | 335.1 (60.4) | 0 | 186.2 (71.9) | 5.3 (5.3) | 0 | 105.3 (67.7) | 4.3 (4.3) | 71.6 (45.2) |
| **Opiliones** | | | | | | | | | | |
| Opiliones sp. | (T) | n.e. | 5.3 (5.3) | n.e. | 0 | 0 | 0 | 1.3 (1.3) | 0 | 0.9 (0.9) |

Table 53. Biomass (mg dry weight $m^{-2}$) of litter- and soil-inhabiting Isopoda, Symphyla, Protura, Diplura, Blattodea, Psocoptera, Homoptera and Opiliones in 1971–72. The August values are not used for calculating "summer" and annual means. Standard error is given within parentheses below the corresponding mean value.
n.e. = not estimated

| | May 17 | June 15 | Aug 4 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|
| Isopoda | | | | | | | | | |
| Porcellionidae sp. | 0 | 0 | n.e. | 0 | 0 | 0 | 0 | 11.84 (11.84) | 3.95 (3.95) |
| Symphyla | | | | | | | | | |
| *Scutigerella* cf. *immaculata* | 0 | 0 | n.e. | 0 | 0 | 0.25 (0.25) | 0.05 (0.05) | 0 | 0.03 (0.03) |
| Protura | | | | | | | | | |
| *Eosentomon* cf. *germanicum* | 0 | 0.03 (0.03) | 0.02 (0.02) | 0.02 (0.02) | 0.03 (0.02) | 0 | 0.02 (0.01) | 0 | 0.01 (0.01) |
| Diplura | | | | | | | | | |
| *Campodea* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.43 (0.43) | 0.14 (0.14) |
| Blattodea | | | | | | | | | |
| *Ectobius lapponicus* | 0 | 0 | n.e. | 0.76 (0.52) | 4.62 (3.49) | 0 | 1.08 (0.90) | 2.59 (2.59) | 1.58 (1.05) |
| Psocoptera | | | | | | | | | |
| Psocoptera sp. | 0.03 (0.03) | 0.03 (0.03) | 0.03 (0.03) | 0.07 (0.05) | 0 | 0 | 0.03 (0.02) | 0 | 0.02 (0.01) |
| Homoptera | | | | | | | | | |
| Coccina sp. | 0 | 1.68 (0.31) | 0 | 0.93 (0.36) | 0.03 (0.03) | 0 | 0.53 (0.34) | 0.02 (0.02) | 0.36 (0.23) |
| Opiliones | | | | | | | | | |
| Opiliones sp. | n.e. | 0.16 (0.16) | n.e. | 0 | 0 | 0 | 0.04 (0.04) | 0 | 0.03 (0.03) |

Table 54. Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) and annual respiration (kcal $m^{-2}$) of litter- and soil-inhabiting Isopoda, Symphyla, Protura, Diplura, Blattodea, Psocoptera, Homoptera and Opiliones in 1971–72. The August values are not used for calculating "summer" and annual means. Standard error is given within parentheses below the corresponding mean value.
+ denotes a value less than 0.0005.
n.e. = not estimated

| | Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) | | | | | | | | | Annual respiration (kcal $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|---|
| | May 17 | June 15 | Aug 4 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual | |
| Isopoda | | | | | | | | | | |
| Porcellionidae sp. | 0 | 0 | n.e. | 0 | 0 | 0 | 0 | 0.046 (0.046) | 0.015 (0.015) | 0.027 (0.027) |
| Symphyla | | | | | | | | | | |
| *Scutigerella* cf. *immaculata* | 0 | 0 | n.e. | 0 | 0 | 0.003 (0.003) | 0.001 (0.001) | 0 | + | 0.001 (0.001) |
| Protura | | | | | | | | | | |
| *Eosentomon* cf. *germanicum* | 0 | 0.004 (0.004) | 0.003 (0.003) | 0.002 (0.002) | 0.002 (0.002) | 0 | 0.002 (0.001) | 0 | 0.001 (0.001) | 0.002 (0.001) |
| Diplura | | | | | | | | | | |
| *Campodea* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.006 (0.006) | 0.002 (0.002) | 0.003 (0.003) |
| Blattodea | | | | | | | | | | |
| *Ectobius lapponicus* | 0 | 0 | n.e. | 0.032 (0.022) | 0.190 (0.130) | 0 | 0.045 (0.037) | 0.019 (0.019) | 0.036 (0.026) | 0.063 (0.045) |
| Psocoptera | | | | | | | | | | |
| Psocoptera sp. | 0.003 (0.003) | 0.003 (0.003) | 0.005 (0.005) | 0.005 (0.004) | 0 | 0 | 0.002 (0.001) | 0 | 0.002 (0.001) | 0.003 (0.002) |
| Homoptera | | | | | | | | | | |
| Coccina sp. | 0 | 0.090 (0.017) | 0 | 0.039 (0.015) | 0.001 (0.001) | 0 | 0.026 (0.018) | + | 0.018 (0.012) | 0.031 (0.021) |
| Opiliones | | | | | | | | | | |
| Opiliones sp. | n.e. | 0.022 (0.022) | n.e. | 0 | 0 | 0 | 0.005 (0.005) | 0 | 0.004 (0.004) | 0.006 (0.006) |

## Discussion

Symphyla, Protura and Diplura are generally considered to be rare animals, and the low abundances and biomasses at Spikbole seem to be in agreement with the common conception of their insignificance. However, relatively large numbers, 1000–10 000 $m^{-2}$ or more, of these groups have been reported in grasslands and cultivated soils by, for example, Salt *et al.* (1948) for Symphyla, Protura and Diplura, Belfield (1956) for Symphyla and Diplura, Raw (1956) for Protura, C.A. Edwards (1958, 1974) for Symphyla and Curry (1969) for Protura. Mean abundances of 11 400–16 000 $m^{-2}$ were recorded for Protura in a Scots pine stand by Axelsson *et al.* (1973b) using identical sampling and extraction techniques as at Spikbole. This indicates that the low abundances estimated at Spikbole, at least of Protura, are real and should not be interpreted as caused by insufficient extraction.

The feeding habits of the taxa presented above are very diverse. The isopod Porcellionidae sp. has been considered as a saprovore/microbivore (cf. Reichle, 1968) as well as the proturan *E.* cf. *germanicum* (cf. Wallwork, 1970), the cockroach *E. lapponicus* and the psocopterans. The symphylan *Scutigerella immaculata* Newp. is known to feed on young roots (Raw, 1967) and has thus been considered as a below-ground herbivore, as also has the Coccina species. The dipluran *Campodea* sp. and the Opiliones sp. have been classified as carnivores (cf. Wallwork, 1970).

# GENERAL DISCUSSION

## Abundance and biomass estimation

One of the most evident problems in estimating soil fauna populations is concerned with separating the animals from the litter and soil. The four separation methods used in the present study complemented each other to a great extent. However, none of the methods was suitable for estimating small, immobile forms such as eggs and small pupae.

The modified Baermann funnel method (O'Connor, 1962) used for extraction of enchytraeids was highly efficient according to Abrahamsen (1972). The hand sorting method was very reliable for large lumbricids (> 0.2 g fw) but less reliable for small ones. Axelsson *et al.* (1971) estimated the hand sorting efficiency to be about 80 % of the total number and 96 % of the total biomass of Lumbricidae in a peat soil (Spikbole) and according to the sorting times the same efficiencies could be presupposed in this study. The hand sorting efficiency was 85–90 % of the total number of larvae (instar V) and pupae of *Phyllobius piri* at Spikbole (Axelsson *et al.*, 1973a), but probably lower for smaller specimens of Coleoptera and Diptera.

The simple Tullgren funnel technique was considered to be sufficient for extracting surface-living and mobile arthropods such as large Collembola, large Acari, Araneae and many Coleoptera. However, most microarthropods are generally believed to be underestimated by simple Tullgren funnels (cf. Forsslund, 1948; Macfadyen, 1961) and are extracted much more efficiently by high gradient canister methods (cf. Macfadyen, *op. cit.*). Marshall (1972) found a significantly higher proportion (73 %) of Collembola extracted by a high gradient apparatus than by Tullgren funnels (45 %). The extraction efficiency of the high gradient canister method ranged from 63 to 98 % for Collembola and Acari in field soil samples afterwards searched for animal corpses (Marshall, *op. cit.*), while the extraction efficiency of the same extraction method was about 80–90 % for Collembola and Acari introduced to defaunated soil cores.

The results of the present study indicated that the reliability of the high gradient canister method varied over the year. Soil-inhabiting Collembola, Acari and some species of Diptera had higher estimates during the "winter" than during the "summer", which was interpreted as being caused by more efficient extraction during the cold season. A sudden increase in numbers should coincide with a corresponding rise in the density of small juveniles owing to hatching, but frequent hatching seemed to be unlikely owing to low temperature during the late autumn and the winter. This was also supported by the size composition of Collembola (Figs. 16–21), which showed a very low proportion of newly hatched specimens during the "winter" and, similarly, a relatively low proportion of juvenile Acari occurred during the same period. A probable explanation of the discrepancy in numbers between the "summer" and the "winter", and especially between the late autumn samplings and the "winter" sampling, was that the soil cores became vertically compressed when the corer cut into the loose peat soil during the "summer" samplings, causing the soil interstices to collapse and the soil-inhabiting animals to become more easily trapped within the cores. During the "winter" the frost maintained the soil structure during the sampling, thus enabling the animals to be sufficiently extracted after the soil had thawed in the high gradient extractor. Assuming the real numbers of Collembola and Acari in October and November to be similar to those in the "winter", and the extraction efficiency to be reduced proportionally over the whole

"summer" period, the real "summer" abundances should be in the region of twice that of the estimated. The same order of underestimation could be reasonably assumed to apply to small Diptera larvae belonging to Sciaridae, Cecidomyiidae and "small" Empididae/Dolichopodidae.

Large and mobile Collembola, Acari and Diptera larvae were more easily extracted than the delicate forms. Since the larger forms contributed proportionally more to the biomass than the smaller ones, the total biomasses of Collembola, Acari and Diptera larvae were probably less underestimated than the abundances, and the real "summer" biomasses of Collembola and Acari, perhaps also of Diptera larvae, should be about 1.5 times those estimated. The biomass estimations involved special problems, e.g. gut content weight, weight loss in preservation fluid and difficulties in weighing microarthropods owing to their small size. These problems have been discussed in more detail for each taxonomic group. A general assumption is, however, that the underestimation of the biomass caused by ethanol preservation before weighing was more important for the final estimates than the overestimation caused by including the gut content in the biomass.

The extraction and separation methods used in this study were among the most reliable for estimating the number and biomass of litter- and soil-dwelling annelids and arthropods. The "winter" estimates seem to have been obtained with high reliability, but since the "summer" extractions were less efficient, the annual mean number of the arthropods should have been about 70 % of the true mean, and for the annelids around 80–90 %. The efficiency of the annual mean biomass was probably around 80–90 % both for the annelids and the arthropods.

Practically all methods of extracting soil animals have limitations in extraction efficiency, and variations in the extraction efficiency from time to time may cause serious misinterpretations of the abundance fluctuations. Confidence in pure abundance data is, therefore, unsatisfactory for many soil animal taxa. The temporal dynamics in the size class composition provide, however, a good check of the reliability of the abundance estimates, since increasing abundances will always coincide with a corresponding increase of juveniles (if no migration occurs). Hence, abundance estimates of animals that are difficult to extract should, if possible, be supported by data on size class structure in order to obtain a sounder basis for conclusions of density fluctuations. This necessitates, of course, studies on the species level.

## Calculation of respiration

The number of published determinations of respiration rates of soil animals has increased considerably during recent years. This, together with the fact that thorough studies of respiration rates are laborious, made it preferable to base the calculations of respiration rates at Spikbole on literature data. However, there was still a lack of data for many taxa which made it necessary to generalize respiration rates from one species to another. It was also necessary to generalize data on certain body weights to other body weights according to allometric equations given for some taxa by, for example, Byzova (1965, 1973), Reichle (1968), Woodland *et al.* (1968), Moulder & Reichle (1972), Wood & Lawton (1973), Jensen & Nielsen (1975) and Luxton (1975), but in other cases scattered information in the literature had to be compiled in order to ob-

tain the respiration data. The relationships between live body weight and oxygen consumption rate used for the taxa occurring at Spikbole are summarized in Table 55. All relationships are adjusted to +10°C in order to make them comparable. Table 55 also shows the ranges of live body weight for which the relationships are valid according to the original references.

The relationships given in Table 55 are presented as regression lines in Fig. 23. The mean regression lines for soil animals given by Reichle (1971) and Ryszkowski (1975) are inserted in the figure after adjustment to +10°C by a $Q_{10} = 2$. Fig. 23 shows that the diplopod *Schizophyllum sabulosum* (based on the values for *Sarmatiulus kessleri*) (line 9) and the acarid groups Ptyctima (line 24), Aptyctima (line 25) and Uropodina (line 23) have low oxygen consumption rates compared with other soil animals of similar body size. Opiliones (line 20), adults of Carabidae and Staphylinidae (line 12), larvae of Staphylinidae and Hydrophilidae (line 13) and Diptera (line 19) show higher oxygen uptake than other animals of comparable body size. At least in some parts of the size range the regression lines for Enchytraeidae (line 1), *Allolobophora rosea* (lines 2–4), *Dendrobaena octaedra* (line 6), Collembola (line 10), Formicidae (line 17), Araneae (line 21) and Gamasina (line 22) fall close to the "mean" lines given by Reichle (*op. cit.*) (line 26) and Ryszkowski (*op. cit.*) (line 27). The low oxygen consumption rates shown by Ptyctima, Aptyctima, Uropodina and *S. sabulosum* probably reflect their high proportion of exoskeleton, which does not contribute to the energy metabolism. Also adult Carabidae and Staphylinidae have a considerable exoskeleton, but they are generally more active animals. Some differences between the oxygen uptake rates may certainly also be attributed to different investigation techniques and different experimental situations. This is clearly demonstrated for adult *Allolobophora rosea* which, after adjustment to +10°C by a $Q_{10} = 2$, had the equation $Q = 47 \cdot W^{0.95}$ according to Byzova (1965) and $Q = 86 \cdot W^{1.0}$ according to Phillipson & Bolton (1976). This implies that an *A. rosea* individual of, say, 0.3 g fw respires 15 $mm^3$ $O_2$ $ind^{-1}$ $h^{-1}$ at +10°C according to Byzova, and 26 $mm^3$ $O_2$ $ind^{-1}$ $h^{-1}$ according to Phillipson & Bolton. The difference in the oxygen uptake data for *A. rosea* according to the different authors is not only of theoretical interest, since *A. rosea* was the most prominent species at Spikbole as regards biomass and respiration and, thus, influenced the total estimates of the annelids considerably. A choice of Byzova's (*op. cit.*) data instead of Phillipson & Bolton's (*op. cit.*) would have led to a reduction from about 63 to 38 kcal $m^{-2}$ $yr^{-1}$ in the respiration figure for *A. rosea* or about 75 to 50 kcal $m^{-2}$ $yr^{-1}$ for total Lumbricidae. This illustrates one of the inevitable weaknesses in the present study, i.e. the dependence on the accuracy of the literature data.

Respirometer data in the literature are predominantly based on adult and large-sized animals, while there is a lack of data for smaller size classes. As a result the relations given in Table 55 and Fig. 23 had to be used outside their validity range, which meant that the respiration rates obtained were generally more uncertain for small specimens of a taxon than for larger ones. This was, for example, demonstrated for Collembola and Acari where a majority of the specimens at Spikbole weighed less than 3 μg live body weight which was outside the validity range for these groups. *A. rosea* was an exception from the general rule since the weight of many *A. rosea* adults at Spikbole exceeded the upper weight range given by Phillipson & Bolton (1976) for this species.

A problem that complicated the calculations of respiration rates was the scarcity of

Table 55. Relationships between live body weight ($W$) and oxygen consumption rate ($Q$) of different soil animal taxa at Spikbole. The relationships are given in the form $Q = a \cdot W^b$, where $Q$ denotes $mm^3$ $O_2$ $ind^{-1}$ $h^{-1}$ and $W$ denotes g live body weight. The relationships are adjusted to +10°C according to various $Q_{10}$ values (see text). The parameters $a$ and $b$ are slightly rounded in comparison with those given earlier in the text. Weight ranges refer to the original references. Number 1–25 refer to the regression lines in Fig. 23.

| Species | Range of live body wt (mg) | $a$ | $b$ | Source of data |
|---|---|---|---|---|
| **Enchytraeidae** | | | | |
| 1. Enchytraeidae (based on *Fridericia* spp. and *Henlea* spp.) | 0.028–14.4 | 19 | 0.67 | Nielsen (1961), O'Connor (1967) |
| **Lumbricidae** | | | | |
| 2. *Allolobophora rosea* juv. $<0.1$ g | 10–100 | 105 | 1.0 | Phillipson & Bolton (1976) |
| 3. *Allolobophora rosea* juv. $>0.1$ g | 100–225 | 97 | 1.0 | " |
| 4. *Allolobophora rosea* ad | 100–350 | 86 | 1.0 | " |
| 5. *Allolobophora caliginosa* | 450–1300 | 42 | 0.91 | Byzova (1965) |
| 6. *Dendrobaena octaedra* (*) | 100–360 | 64 | 0.71 | " |
| 7. *Lumbricus rubellus* | 390–1100 | 50 | 0.84 | " |
| **Isopoda** | | | | |
| 8. Porcellionidae (based on *Metoponorthus pruinosus*) | 18.4 | 88 | 0.84 | Reichle (1968) |
| **Diplopoda** | | | | |
| 9. *Schizophyllum sabulosum* (based on *Sarmatiulus kessleri*) | 24–730 | 18 | 0.73 | Byzova (1973) |
| **Collembola** | | | | |
| 10. Collembola (*) | 0.003–6.61 | 29 | 0.73 | see text |
| **Blattodea** | | | | |
| 11. *Ectobius lapponicus* (based on *Blattella germanica*) | 3.6–26 | 74 | 0.70 | Woodland *et al* (1968) |
| **Coleoptera** | | | | |
| 12. Carabidae and Staphylinidae ad. (*) | 1.2–664 | 113 | 0.74 | see text |
| 13. Staphylinidae and Hydrophilidae larvae (*) | 1–8 | 141 | 0.77 | Byzova (1973) |
| 14. Elateridae larvae (based on *Agriotes lineatus*) | 20–37 | 53 | 0.80 | Prokopeva (1968), see text |
| 15. Curculionidae larvae (based on *Phyllobius piri*) | 5.6–22 | 89 | 0.80 | Larsson (unpubl.) |
| 16. *Phyllobius piri* pupae | 17–21 | 35 | 0.80 | Larsson & Lohm (1975) |
| **Hymenoptera** | | | | |
| 17. Formicidae | 0.8–22.4 | 115 | 1.0 | Jensen & Nielsen (1975) |
| **Diptera** | | | | |
| 18. Tipulidae larvae (based on *Tipula scripta* and *T. peliostigma*) | 30–270 | 46 | 0.52 | Byzova (1973) |
| 19. Diptera larvae (less Tipulidae) | 0.01–62 | 210 | 0.87 | see text |
| **Opiliones** | | | | |
| 20. Opiliones (based on *Leiobunum rotundum*) | 0.3–32 | 251 | 0.79 | Phillipson (1963) |
| **Araneae** | | | | |
| 21. Araneae (based on Lycosidae) | 17–633 | 90 | 0.92 | Moulder & Reichle (1972) |
| **Acari** | | | | |
| 22. Gamasina (*) | 0.008–0.45 | 102 | 0.87 | Wood & Lawton (1973) |
| 23. Uropodina | 0.009–0.16 | 5.0 | 0.67 | " |
| 24. Ptyctima (Cryptostigmata) | 0.025–0.75 | 3.5 | 0.69 | Luxton (1975) |
| 25. Aptyctima (Cryptostigmata) | 0.010–0.25 | 7.2 | 0.69 | " |

(*) Relationship no. 6 also used for *Dendrobaena rubida*, no. 10 also used for Symphyla, Protura, Diplura, Psocoptera, Coccina and Hymenoptera Parasitica, no. 12 also used for adults of *Megasternum*, *Choleva*, *Atomaria*, *Corticaria* and *Corticarina*, no. 13 also used for larvae of Cantharidae, *Lagria* and Coleoptera sp., and no. 22 also used for Prostigmata and Astigmata.

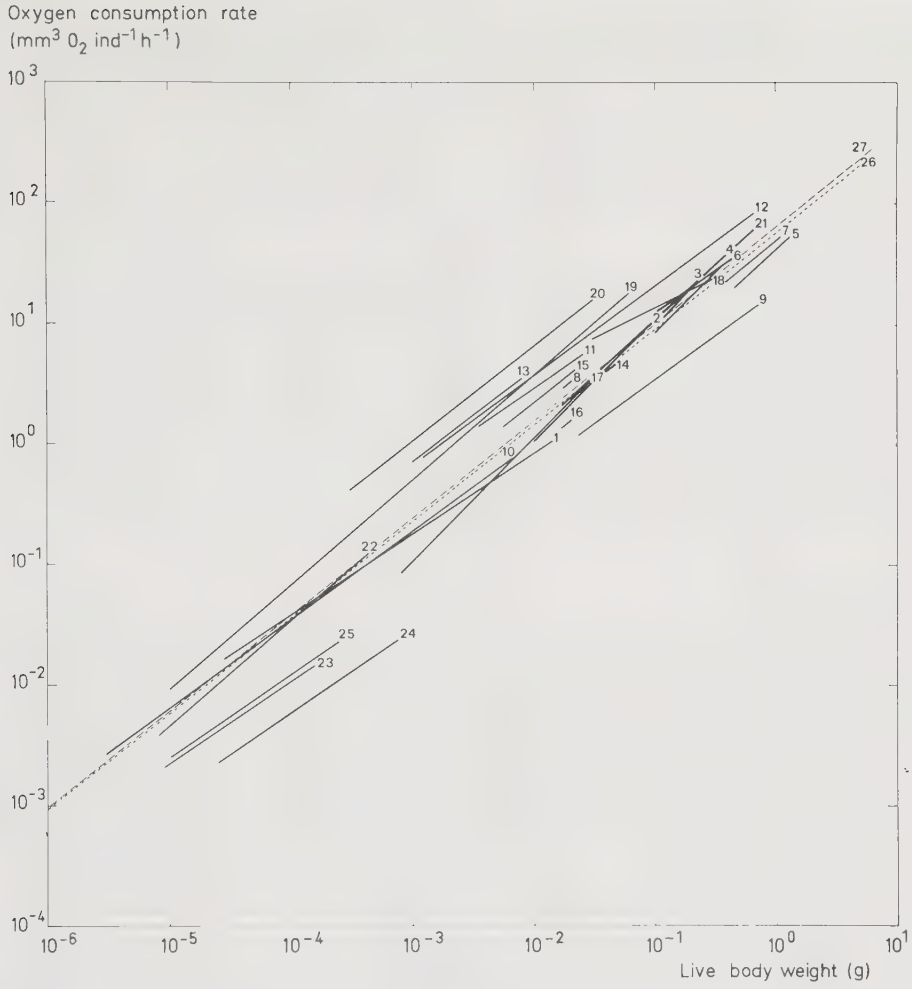


**Figure 23.** The relationship between live body weight and oxygen consumption rate per individual at +10°C for the 25 soil animal taxa listed in Table 55. The relationships are adjusted to +10°C according to different $Q_{10}$ values (see text). The mean relationships for soil animals, $Q = 63.6 \cdot W^{0.808}$ at +10°C derived from Reichle (1971), and $Q = 69.4 \cdot W^{0.813}$ at +10°C derived from Ryszkowski (1975), are given for comparison (lines 26 and 27, respectively).

data at low temperatures. Only a limited number of studies have been performed at temperatures below +5°C (e.g. Berthet, 1964; Zinkler, 1966; Tilbrook & Block, 1972; Schauermann, 1973; Block & Tilbrook, 1975; Larsson & Lohm, 1975) and, therefore, the adjustment of respiration rates to low temperatures had sometimes to be based on insufficient material. The $Q_{10}$ values were generally assumed to increase with decreasing temperature, but it is possible that the $Q_{10}$ values of about 3 or 4 between −0.9 and +5°C were too low, thus causing an overestimation of the November and "winter" respirations.

The annual respiration figures were affected both by the population estimates and the respiration rates adjusted to the field temperatures. The earlier discussion showed that the calculation of respiration rates involves many steps of generalization, e.g. a generalization of the laboratory situation to the field, to other body weights and to other temperatures. It is impossible to evaluate whether these calculations caused an over- or underestimation of the respiration rates. It is, however, probable that errors introduced in the calculation of respiration rates were more significant for the final respiration figures than the errors originating from the sampling procedure or from the inefficient extractions.

## Dominant species

The most abundant species among the annelids and arthropods at Spikbole was *Tullbergia krausbaueri* with an annual mean density of about 65 000 individuals $m^{-2}$ before correction for insufficient extraction. Most of the numerically dominant species belonged to Collembola and Acari, and only two enchytraeid species, *Henlea perpusilla* and *H. ventriculosa*, and one Diptera species, *Bibio nigriventris*, could be placed among the 20 most abundant species at Spikbole (Table 56). Some reservations must be made, since Prostigmata consisted of several abundant forms that were not determined to the species level, and the ranking of the enchytraeid species was uncertain due to identification difficulties (cf. Enchytraeidae).

The annelid and arthropod biomass at Spikbole was dominated by the lumbricid *Allolobophora rosea* which had an annual mean biomass of 5.0 g dw $m^{-2}$ and the weevil *Phyllobius piri* which had an annual mean of 2.2 g dw $m^{-2}$. Other species contributed much less to the total biomass. Larger species seemed to have a greater influence on the biomass than smaller ones, and it is striking that all lumbricid species, even the sparsely occurring *Dendrobaena rubida*, had a higher biomass than any of the Collembola and Acari species (Table 56). The estimates of the biomasses of the enchytraeid species are very uncertain, but it is probable that *Fridericia ratzeli* was the third dominant species in the soil at Spikbole. The biomass of *Pergamasus brevicornis* includes part of the deutonymphal weight of *P. brevicornis/septentrionalis*.

The annual respiration was, like the biomass, dominated by *A. rosea* and *P. piri* which respired 63 and 24 kcal $m^{-2}$ $yr^{-1}$, respectively. Their dominance in respiration was, however, much less pronounced than their dominance in biomass, since *F. ratzeli* respired as much as 20 kcal $m^{-2}$ $yr^{-1}$ (based on assumptions of abundance and biomass) and *B. nigriventris* 16 kcal $m^{-2}$ $yr^{-1}$. Table 56 shows that relative to the biomass the respiration was lower for large species, e.g. *A. rosea*, *A. caliginosa* and *Lumbricus rubellus*, and higher for small species, such as *Henlea perpusilla* and many Collembola, which is

Table 56. List of the 20 dominant annelid and arthropod species at Spikbole, concerning annual mean abundance, annual mean biomass and annual respiration during 1971–72. The figures for the enchytraeid species are approximate (see text). The list is incomplete as regards some Prostigmata (abundance) and Diptera species (biomass and respiration) owing to identification problems. ad = adults l = larvae p = pupae

| | Abundance no. $m^{-2}$ | | Biomass g dry wt $m^{-2}$ | | Respiration kcal $m^{-2}$ $yr^{-1}$ | |
|---|---|---|---|---|---|---|
| 1. | *Tullbergia krausbaueri* (Collembola, Onychiuridae) | 65 000 | *Allolobophora rosea* (Oligochaeta, Lumbricidae) | 4.980 | *Allolobophora rosea* (Oligochaeta, Lumbricidae) | 63.08 |
| 2. | *Folsomia quadrioculata* (Collembola, Isotomidae) | 14 600 | *Phyllobius piri* l+p (Coleoptera, Curculionidae) | 2.234 | *Phyllobius piri* l+p (Coleoptera, Curculionidae) | 23.90 |
| 3. | *Brachychochthonius immaculatus* (Acari, Brachychthoniidae) | 14 000 | *Fridericia ratzeli (***)* (Oligochaeta, Enchytraeidae) | 0.60 | *Fridericia ratzeli* (Oligochaeta, Enchytraeidae) | 20 |
| 4. | *Schwiebea cavernicola* (Acari, Acaridae) | 12 900 | *Lumbricus rubellus* (Oligochaeta, Lumbricidae) | 0.370 | *Bibio nigriventris* l (Diptera, Bibionidae) | 15.77 |
| 5. | *Henlea perpusilla (*)* (Oligochaeta, Enchytraeidae) | 11 900 | *Allolobophora caliginosa* (Oligochaeta, Lumbricidae) | 0.303 | *Henlea perpusilla* (Oligochaeta, Enchytraeidae) | 10 |
| 6. | *Isotoma notabilis* (Collembola, Isotomidae) | 11 400 | *Dendrobaena octaedra* (Oligochaeta, Lumbricidae) | 0.236 | *Henlea ventriculosa* (Oligochaeta, Enchytraeidae) | 6 |
| 7. | *Tectocepheus sarekensis* (Acari, Tectocepheidae) | 9 000 | *Agriotes lineatus/obscurus* l (Coleoptera, Elateridae) | 0.232 | *Dendrobaena octaedra* (Oligochaeta, Lumbricidae) | 4.88 |
| 8. | *Oppia minus* (Acari, Oppiidae) | 7 500 | *Bibio nigriventris* l (Diptera, Bibionidae) | 0.227 | *Lumbricus rubellus* (Oligochaeta, Lumbricidae) | 3.67 |
| 9. | *Isotomiella minor* (Collembola, Isotomidae) | 5 500 | *Henlea perpusilla (*)* (Oligochaeta, Enchytraeidae) | 0.12 | *Agriotes lineatus/obscurus* l (Coleoptera, Elateridae) | 2.84 |
| 10. | *Oppia nova* (Acari, Oppiidae) | 4 500 | *Henlea ventriculosa (**)* (Oligochaeta, Enchytraeidae) | 0.10 | *Allolobophora caliginosa* (Oligochaeta, Lumbricidae) | 2.62 |
| 11. | *Henlea ventriculosa (**)* (Oligochaeta, Enchytraeidae) | 3 600 | *Phyllobius viridicollis* l+p (Coleoptera, Curculionidae) | 0.081 | *Phyllobius viridicollis* l+p (Coleoptera, Curculionidae) | 2.14 |
| 12. | *Liochthonius sellnicki* (Acari, Brachychthoniidae) | 3 000 | *Dendrobaena rubida* (Oligochaeta, Lumbricidae) | 0.042 | *Tullbergia krausbaueri* (Collembola, Onychiuridae) | 1.49 |
| 13. | Tarsonemidae sp. (Acari, Tarsonemidae) | 2 900 | *Calathus melanocephalus* l+ad (Coleoptera, Carabidae) | 0.037 | *Calathus melanocephalus* l+ad (Coleoptera, Carabidae) | 1.44 |
| 14. | *Bibio nigriventris* l (Diptera, Bibionidae) | 2 800 | *Isotoma viridis* (Collembola, Isotomidae) | 0.030 | *Megasternum boletophagum* l+ad (Coleoptera, Hydrophilidae) | 1.28 |
| 15. | *Folsomia fimetaria* coll. (Collembola, Isotomidae) | 2 800 | *Schizophyllum sabulosum* (Diplopoda, Iulidae) | 0.029 | *Folsomia quadrioculata* (Collembola, Isotomidae) | 1.12 |
| 16. | *Lepidocyrtus cyaneus* (Collembola, Entomobryidae) | 2 000 | *Symphoromyia crassicornis* l (Diptera, Rhagionidae) | 0.029 | *Symphoromyia crassicornis* l (Diptera, Rhagionidae) | 0.93 |
| 17. | *Entomobrya nivalis* (Collembola, Entomobryidae) | 1 800 | *Pergamasus brevicornis* (Acari, Parasitidae) | 0.026 | *Dendrobaena rubida* (Oligochaeta, Lumbricidae) | 0.92 |
| 18. | *Mixozercon sellnicki* (Acari, Zerconidae) | 1 700 | *Folsomia quadrioculata* (Collembola, Isotomidae) | 0.024 | *Lagria hirta* l (Coleoptera, Lagriidae) | 0.82 |
| 19. | *Histiostoma* cf. *feroniarum* (Acari, Anoetidae) | 1 700 | *Tullbergia krausbaueri* (Collembola, Onychiuridae) | 0.024 | *Isotoma notabilis* (Collembola, Isotomidae) | 0.82 |
| 20. | *Rhodacarellus silesiacus* (Acari, Rhodacaridae) | 1 300 | *Megasternum boletophagum* l+ad (Coleoptera, Hydrophilidae) | 0.020 | *Isotoma viridis* (Collembola, Isotomidae) | 0.76 |

* assumed to account for 50 % of abundance and 14 % of biomass of Enchytraeidae
** assumed to account for 15 % of abundance and 12 % of biomass of Enchytraeidae
*** assumed to account for 5 % of abundance and 70 % of biomass of Enchytraeidae

in agreement with the general relationships given in Table 55. According to these relationships (cf. Fig. 23), Carabidae, Hydrophilidae and Diptera had higher rates than most other soil animals of similar size; here reflected in a larger contribution to the annual respiration. Different life cycles also affected annual respiration in relation to biomass, since according to the $Q_{10}$ relationships a high biomass during the summer contributed much more to the annual respiration than during the winter. *P. piri* and *P. viridicollis* were, for example, not present in the soil in June and, therefore, their respiration figures were relatively lower compared with species with permanent stages in the soil. The relatively low annual respiration of *P. piri* was also explained by the long pupal stage with a low respiration rate.

The annual respiration was dominated by saprovorous/microbivorous species, such as *A. rosea, F. ratzeli, B. nigriventris* and the *Henlea* species. Among the 20 most dominant species (Table 56) the below-ground herbivores were represented by three species, namely *P. piri, Agriotes lineatus/obscurus* and *P. viridicollis.* The below-ground carnivores were represented by four species, namely, *Calathus melanocephalus, Megasternum boletophagum* (of which the larvae were considered as carnivores, respiring 1.0 kcal $m^{-2}$ $yr^{-1}$), *Symphoromyia crassicornis* and *Lagria hirta*. Some of the Empididae (carnivores) and Muscidae (probably saprovore/microbivores) species might also have been placed among the 20 dominant annelids and arthropods with regard to respiration if they had been identified to species.

## Seasonal fluctuations

The abundance and biomass of the annelids and arthropods at Spikbole fluctuated more or less pronouncedly over the year. The most conspicuous fluctuations were found for species with simultaneous hatching and with well separated generations, such as many Coleoptera and Diptera species. This type of development was shown by, for example, the weevil *Phyllobius piri* that had a one-year life cycle at Spikbole. The peak number of *P. piri* larvae was reached in July after completed egg-hatching (cf. Axelsson *et al.*, 1973a) after which the number declined successively owing to mortality (Fig. 24). The adults emerged from the soil at the end of May, implying that the species was not present in the soil until oviposition occurred in late June. The *P. piri* larvae increased in weight up to pupation in early October, causing the maximum biomass to be recorded considerably later than the maximum abundance (cf. Fig. 24).

The seasonal fluctuations in abundance and biomass were less distinct for species with protracted hatching periods (e.g. some Collembola) or with life cycles lasting more than one year (e.g. Lumbricidae, Diplopoda, Elateridae). Seasonal fluctuations of larger taxa (families, orders) were, moreover, less pronounced than of those of individual species (cf. Tables 61 and 62), since larger taxa often consisted of species with non-synchronous life cycles. Coleoptera, for example, consisted of a large number of species with different phenological patterns. Some Coleoptera, e.g. Cantharidae sp. and Coleoptera sp., were found as newly hatched larvae in June, while young larvae of *Megasternum boletophagum* and *Lagria hirta* were found in dense numbers in September. Nevertheless, the dominance of the latter species together with some others caused the peak abundance of total Coleoptera (less *P. piri*) in the early autumn (Fig. 24). The small fluctuations in the biomass of Coleoptera (less *P. piri*) are partly explained by the dominance of

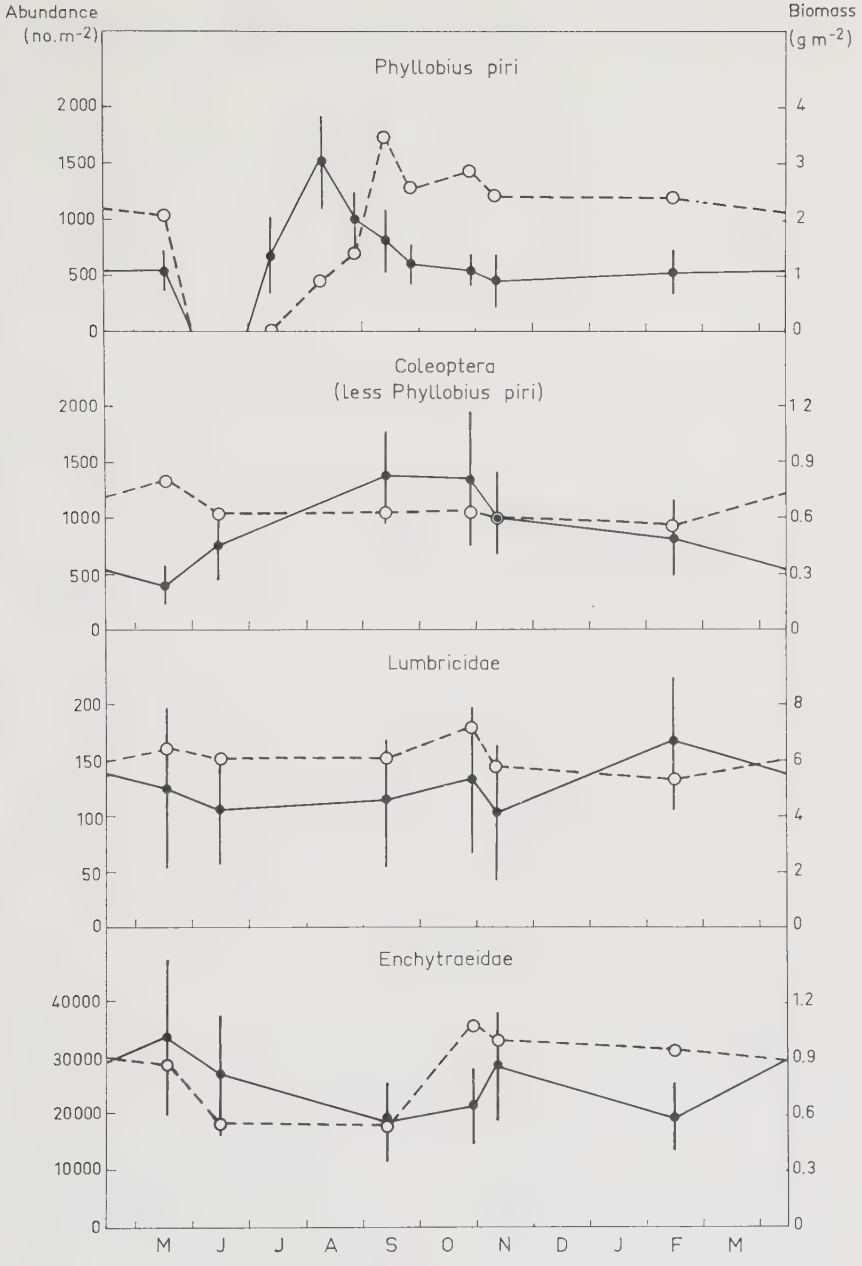


**Figure 24.** Fluctuations in abundance (given as 95 % confidence interval) and biomass (in dry weight) of larvae and pupae of *Phyllobius piri*, Coleoptera less *P. piri*, Lumbricidae and Enchytraeidae in 1971–72. The abundances (solid lines) and biomasses (broken lines) are connected assuming equal values from year to year. Data on *P. piri* mainly obtained from Axelsson *et al.* (1973a).

*Agriotes lineatus* and *A. obscurus*. The larval stages of these elaterids have a duration of 4–5 years, and the contemporaneous presence of several generations of these larvae buffered all dramatic changes in the total biomass of Coleoptera (less *P. piri*).

The seasonal fluctuations in number as well as in biomass were small for Lumbricidae (Fig. 24) which, like the Elateridae, have life cycles lasting several years in the soil. The size class distribution of the dominant lumbricid, *Allolobophora rosea*, indicated that a considerable part of the hatching occurred during the autumn, which is in agreement with the results of Rundgren (1977). However, the occurrence of small juveniles was almost masked in the total abundance owing to the large number of individuals belonging to older generations. The biomass of *A. rosea* and, consequently, the biomass of total Lumbricidae was dominated by the large adults (Table 11) and no seasonal fluctuations in biomass could be demonstrated with certainty (Fig. 24).

The enchytraeids were not separated into species or size-classes, and it is, therefore, difficult to draw any conclusions about the population dynamics reflected by the fluctuations in total number and biomass. A possible interpretation of the data is that there was a pronounced spring and early summer hatching and an additional autumn hatching (Fig. 24). The spring generation was probably reduced in numbers but increased in weight during the summer and autumn, and high biomasses were, therefore, obtained in October and November. The relatively high biomass in May was probably caused by hibernating large enchytraeids that did not survive up to the June sampling when the lowest mean body weight was obtained.

The abundances of Collembola, Acari and Diptera (less *Bibio nigriventris*) were estimated to be higher during the "winter" that at any of the "summer" samplings (cf. Table 61). However, according to the earlier discussion the real "summer" abundances should be two-fold those estimated, while the corresponding biomasses should be 1.5 times higher. The adjusted and probably more realistic abundances and biomasses of Collembola, Acari and Diptera (less *B. nigriventris* that had a very aggregated distribution) are given in Fig. 25, where the empirically found data are also given for comparison. Also the confidence intervals of the adjusted abundances were redoubled in Fig. 25, and the abundance curves are drawn within the extended confidence limits. The abundance and biomass curves express the authors' conception of the fluctuation patterns and must be considered as hypothetical.

Different Collembola species showed different phenological patterns. *Folsomia quadrioculata* had, for example, a distinct spring and early summer hatching. *Entomobrya nivalis* showed a density peak in June coinciding with a large number of small juveniles, while *Isotoma notabilis* seemed to have a more extended hatching period. The very dominance of *Tullbergia krausbaueri* with a great proportion of small juveniles in August and September caused, however, the peaks and lows of the other species to be masked in the total abundance, and the peak abundance of total Collembola probably occurred in August (Fig. 25). The biomass fluctuations were difficult to interpret, but maximum biomass seemed to occur during the autumn somewhat after the density peak and or in the late spring. The biomass low in June was probably preceded by the disappearance of old adults from the previous year's generation.

The hatching period of Acari seemed to last from about June to October according to the frequent appearance of juveniles. Most gamasids hatched in June which coincided with a distinct density peak. Also Brachychthoniidae had a high proportion of juve-

niles in June, but the highest numbers of juvenile brachychthoniids were obtained in August. The prostigmatids also showed a density peak in August and since Prostigmata and Brachychthoniidae were numerically dominant taxa within Acari, their contribution to the total abundance of Acari should give rise to a peak abundance during the summer (cf. Fig. 25). The most abundant species were generally very small and had a limited influence on the total biomass. The acarine biomass was dominated by the large-sized gamasids, and especially by the *Pergamasus* species. This explains why the total biomass of Acari was in a low in June, when the gamasids and many other taxa were found as small juveniles, and in a peak in the late autumn, when the *Pergamasus* species began to reach maturity.

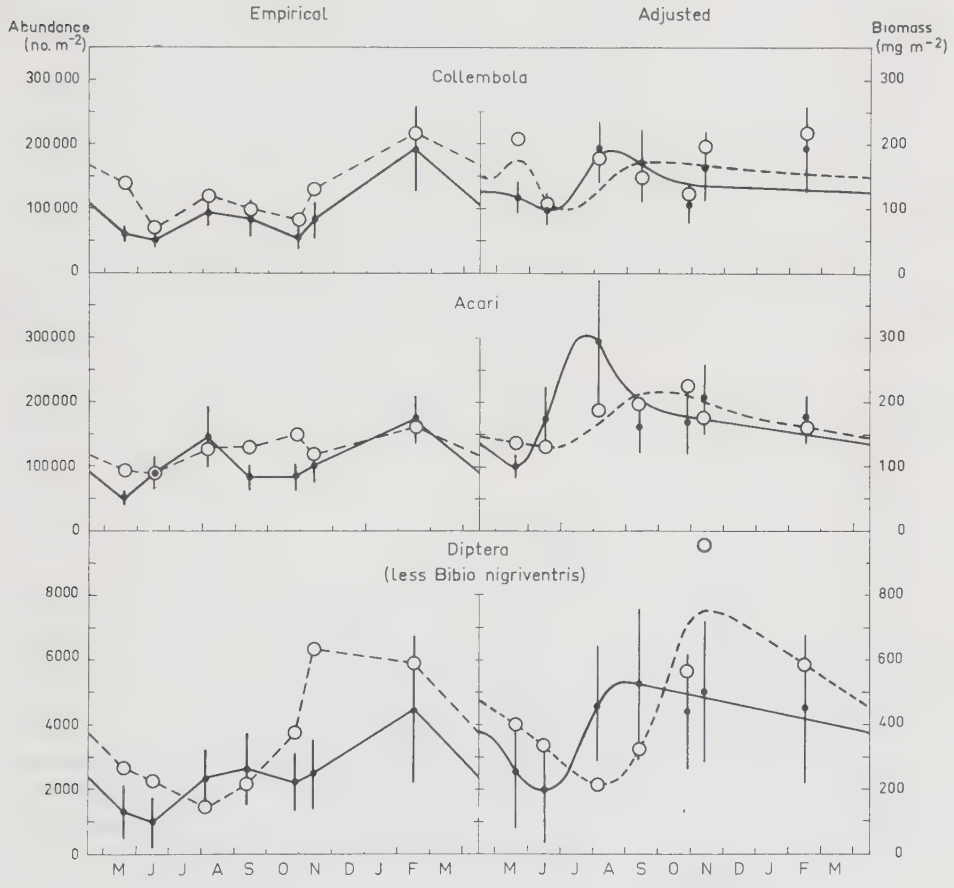


**Figure 25.** Fluctuations in abundance (given as 95 % confidence interval) and biomass (in dry weight) of Collembola, Acari, and larvae and pupae of Diptera less *Bibio nigriventris* before and after adjustment on account of inefficient extraction during the "summer" samplings. The abundances (solid lines) and biomasses (broken lines) are connected assuming equal values from year to year. The adjusted abundances are two-fold those estimated and the adjusted biomasses are 1.5 times those estimated.

Many Diptera species at Spikbole seemed to have a univoltine developmental pattern with an above-ground period as adults during the summer, followed by eggs, larvae and pupae during the autumn, winter and spring. Some species, predominantly belonging to Cecidomyiidae, Sciaridae and Chironomidae, diverged from the uniformity, causing the seasonal fluctuations in abundance and biomass to be less pronounced for total Diptera than for the individual species. The general pattern was, nevertheless, that Diptera showed an abundance peak and a biomass low in the late summer, when most larvae had hatched but were still small, and a biomass peak in the late autumn, when the larvae began to become fully grown (Fig. 25).

The seasonal fluctuations in the total abundance and biomass of the below-ground annelids and arthropods at Spikbole were dominated by only a few large taxa. Collembola and Acari dominated the abundance and caused the total annelid and arthropod community to have a density minimum in late spring (May) and a density maximum in late summer (August). Enchytraeidae were considerably less abundant than Collembola and Acari, and their density peaks in the late spring and in the autumn were masked in the total abundance because of the dominance of the two microarthropod taxa. Lumbricidae and Coleoptera dominated the biomass, but since Lumbricidae did not fluctuate significantly over the year, the biomass changes were mainly attributed to Coleoptera and in particular to *Phyllobius piri*, which had a summer minimum and an autumn maximum in the biomass. Other dominant taxa, such as Enchytraeidae, Diptera, Collembola and Acari, showed a similar pattern in the biomass fluctuations and, therefore, the total below-ground annelid and arthropod community had a biomass minimum in the mid-summer period (June/July) and a biomass maximum in the autumn (October) (cf. Table 62). Owing to a high temperature, the respiration rates per unit weight were considerably higher during the summer than during the other seasons. The comparatively low biomass in the summer counteracted, however, the effect of the temperature and caused the daily respiration figures to fluctuate more moderately over the year than in case of a constant biomass (cf. Table 63).

## Comparison with other grasslands

The annelid and arthropod fauna are numerically dominated by Collembola and Acari in most temperate grasslands. The annual mean abundance of about 110 000 $m^{-2}$ of Collembola at Spikbole is similar to some of the highest annual means reported from grassland soils (Haarlov, 1960; Curry, 1969). The annual mean of about 110 000 $m^{-2}$ of Acari is also a fairly high estimate, but annual means up to 180 000 $m^{-2}$ have been recorded for grasslands (cf. Curry, 1969). Acari is more abundant than Collembola in many habitats. This dominance is very pronounced in mor soils, but in grassland soils the numbers of these two taxa are usually of the same magnitude (e.g. Lebrun, 1971) and this was also demonstrated at Spikbole. The annual mean of 24 000 $m^{-2}$ of Enchytraeidae seems to be slightly lower than normally reported from grasslands in northwestern Europe (Nielsen, 1955b, 1961; Peachey, 1963; Möller, 1969; Springett, 1970), and this taxon can sometimes attain densities that exceed those of Collembola and Acari (cf. Cragg, 1961). The annual means of Diptera (5500 $m^{-2}$) and Coleoptera (1400 $m^{-2}$) at Spikbole are high in view of other investigations. Higher estimates of Diptera have only been reported from deciduous woods (Healey & Russell-Smith, 1970, 1971), and

higher estimates of Coleoptera have only been found in grasslands comprising large populations of species known as agricultural pests (e.g. Salt & Hollick, 1944; Salt *et al.*, 1948). The annual mean of around 200 $m^{-2}$ for Araneae is a common estimate for unmanaged temperate grasslands (e.g. Duffey, 1962; Cherrett, 1964; Delchev & Kajak, 1974), and the annual mean of 130 $m^{-2}$ for Lumbricidae is slightly lower than usually found in various grasslands (e.g. Nordström & Rundgren, 1973; Nowak, 1975; Curry, 1976).

Temperate grasslands in Europe are often dominated by lumbricids as regards the biomass. A lumbricid dominance was also found at Spikbole where this taxon accounted for 56 % of the annual mean annelid and arthropod biomass. The annual mean of nearly 6 g dw $m^{-2}$ of Lumbricidae at Spikbole is a common figure for temperate grasslands, although higher biomasses have often been estimated in base-rich grasslands and localities with higher precipitation (Satchell, 1967; Edwards & Lofty, 1972; Nordström & Rundgren, 1973). The annual mean biomass of about 3 g dw $m^{-2}$ of Coleoptera at Spikbole is very high in comparison with literature data, but these data, however, are scanty. Enchytraeidae had an annual mean of 0.85 g dw $m^{-2}$ which falls within the normal range of biomasses in grassland ecosystems (e.g. Nielsen, 1955b, 1961; Möller, 1969). The annual mean biomass of 0.65 g dw $m^{-2}$ of Diptera at Spikbole is a relatively high figure, higher biomasses of Diptera being estimated in high-altitude and arctic grasslands with large populations of Tipulidae larvae (e.g. Cragg, 1961; Hofsvang, 1972; Chernov *et al.*, 1975). The annual mean biomass of 0.14 g dw $m^{-2}$ of Collembola is a fairly normal estimate in comparison with many other grasslands (e.g. Macfadyen, 1952; Hale, 1966), while the annual mean of 0.13 g dw $m^{-2}$ of Acari is lower than most other estimates (e.g. Block, 1966a; Lebrun, 1971).

The lumbricids have lower respiration rates per unit weight than most other soil invertebrates, but owing to their dominance in biomass in many grasslands their annual respiration often exceeds those of other taxa. This was, for example, demonstrated at Spikbole where Lumbricidae contributed 38 % of the below-ground annelid and arthropod respiration of 200 kcal $m^{-2}$ $yr^{-1}$, while Enchytraeidae and Coleoptera each contributed 21 % and Diptera contributed 15 %. The annual respiration figures of both Lumbricidae (75 kcal $m^{-2}$ $yr^{-1}$) and Enchytraeidae (about 40 kcal $m^{-2}$ $yr^{-1}$) both fall within the medium or lower part of the range of annual respirations reported for other temperate grasslands (e.g. Nielsen, 1961; Macfadyen, 1963; Möller, 1969). The annual respiration of about 40 kcal $m^{2}$ $yr^{-1}$ of Coleoptera is comparatively high, probably due to the scarcity of respiration data on this taxon. The Diptera respiration of about 30 kcal $m^{-2}$ $yr^{-1}$ at Spikbole is also high in comparison with other temperate grasslands. The annual respiration figures of Collembola (about 6 kcal $m^{-2}$ $yr^{-1}$) and Acari (about 3 kcal $m^{-2}$ $yr^{-1}$) are very low in relation to the values reported by Macfadyen (1963) for a grazed meadow in England. However, more recent studies on Collembola (e.g. Healey, 1967a, b; Dunger, 1968; Tanaka 1970b; Huhta & Koskenniemi, 1975) indicate a less significant role of Collembola in the energy release than suggested by Macfadyen (*op. cit.*). Recent data on Gamasina (Webb, 1970a; Wood & Lawton, 1973) also indicate that Macfadyen's (*op. cit.*) estimates of Parasitidae were too high, resulting in an overestimation of the respiration of total Acari.

This brief comparison with other grasslands indicates that the abundance, biomass and respiration of the different below-ground annelid and arthropod taxa at Spikbole

resembles those at a number of other sites. This is noteworthy since Spikbole has only recently developed into a grassland (cf. Site description, p. 15), and since the grasslands used in the comparison cover a wide range of moisture conditions, chemical and physical properties, management and altitudes. On the other hand, the similarity in food resources (grass roots, grass litter) constitutes a similar basis for establishment of the same type of soil fauna.

# ABOVE-GROUND FAUNA

## INTRODUCTION

Rejecta (faeces and excreta) and carcasses (dead animals) from the above-ground fauna provide an energetical contribution to the saprovorous organisms in the litter and soil. This contribution is generally small in comparison with the input of dead plant matter but may be considerable in pastures grazed by cattle (Macfadyen, 1963) or sheep (Kajak, 1974), or in areas with heavy outbreaks of defoliating insects (Rafes, 1970). It was believed that the contribution from the above-ground fauna at Spikbole could not be very large but, nevertheless, an attempt was made to estimate the production of rejecta and carcasses of the above-ground arthropods. The estimates were based on respiration estimates from which production and egestion values were derived according to efficiency quotients given by Heal & MacLean (1975).

## METHODS

Macroarthropod and lumbricid sample units were used to estimate the population sizes of the above-ground arthropods. The corresponding extraction methods are indicated in Table 58. Smaller arthropods were attributed mean weights after weighing subsamples of catches. The mean weights obtained were 0.004 mg dw for Thysanoptera, 0.05 mg dw for Aphidina and 0.10 mg dw for Cicadina, juvenile Heteroptera and adult Diptera. Other arthropods were weighed individually to the nearest 0.01 mg. The dry weight/live weight ratio was assumed to be 0.25 for Cicadina, Aphidina, Heteroptera, Symphyta larvae and Lepidoptera larvae, 0.32 for Thysanoptera (Edwards, 1967) and 0.33 for adult Coleoptera (cf. p. 82), adult Diptera and pupal Symphyta.

The oxygen consumption rates of the above-ground arthropods at Spikbole were calculated according to the relationships summarized in Table 57, assuming the same daily mean temperatures as given for the below-ground fauna. The oxygen consumption rates of Thysanoptera were calculated from the results given by Vasiliu & Burclau (1970) for *Aeolothrips intermedius* Bagn. and by Steigen (1975a) for *Anaphothrips secticornis* (Trybom). Vasiliu & Burclau (*op. cit.*) found a respiration rate of 19.0 cal $g^{-1}$ $h^{-1}$ at +15.5°C,

Table 57. The relationship between live body weight ($W$) and oxygen consumption rate ($Q$) of different above-ground arthropods at a given temperature. The relationship is of the form $Q = a \cdot W^b$, where $Q$ denotes mm$^3$ $O_2$ ind$^{-1}$ h$^{-1}$ and $W$ denotes g live body weight. Adjustments to other temperatures are indicated by the corresponding $Q_{10}$ value.
ad = adults l = larvae p = pupae

| | $a$ | $b$ | Temp. (°C) | $Q_{10}$ | Actual temp. int. |
|---|---|---|---|---|---|
| Thysanoptera | 124 | 0.80 | 8 | 4 | (-0.9 – 10.3°) |
| Cicadina | (see text) | | 10 | 4 | (-0.9 – 10.3°) |
| Aphidina | 207 | 0.657 | 18 | 4 | (-0.9 – 18.0°) |
| Heteroptera, Cantharidae ad, | 390 | 0.80 | 20 | 3 | ( 5.0 – 20.0°) |
| Coccinellidae ad, Chrysomelidae ad | | | | 4 | (-0.9 – 5.0°) |
| Elateridae ad | (see text) | | 12 | 4 | ( 5.0 – 12.0°) |
| Curculionidae ad | 40 | 0.70 | 10 | 3 | ( 5.0 – 10.3°) |
| Lepidoptera l, Symphyta l+p | 290 | 0.7665 | 15 | 4 | (-0.9 – 15.0°) |
| Diptera ad | (see text) | | 25 | 3 | ( 5.0 – 25.0°) |
| | | | | 4 | (-0.9 – 5.0°) |

and their results at +12 and +5°C indicated a $Q_{10}$ = 4.0 in this temperature range. Steigen (*op. cit.*) obtained a respiration rate of 1.51 mm$^3$ $O_2$ mg$^{-1}$ dw h$^{-1}$ at +8°C and a $Q_{10}$ = 2.44 between +8 and +18°C. When the data were adjusted to +8°C and given in a similar form, Vasiliu & Burclau's (*op. cit.*) figures were nearly three times higher than those by Steigen (*op. cit.*). Assuming the exponent $b$ to be 0.80 (cf. Table 57), a mean of these data corresponds to the equation $Q = 124 \cdot W^{0.80}$ at +8°C. The rates calculated from this equation were adjusted to other temperatures by assuming a $Q_{10}$ = 4.

The mean body weight of 0.10 mg dw of Cicadina at Spikbole is similar to that of the second instar of *Neophilaenus lineatus* (L.) according to Hinton (1971). Hinton (*op. cit.*) recorded an oxygen consumption rate of 0.164 mm$^3$ $O_2$ ind$^{-1}$ h$^{-1}$ at +10°C for this instar, and this rate was also used for calculation of the oxygen consumption of Cicadina at Spikbole after adjustment to different field temperatures by a $Q_{10}$ = 4.

Dixon (1973) has estimated the relationship between oxygen consumption rate and fresh weight of the aphid *Drepanosiphum platanoides* (Schr.) previously kept at +18°C for seven days. In a slightly modified form this relationship was $Q = 207 \cdot W^{0.657}$ at +18°C as shown in Table 57. The oxygen consumption rates of the Aphidina at Spikbole were calculated from this equation after adjustment to other temperatures by a $Q_{10}$ = 4.

Edwards (1946) found that smaller adults of *Melanotus communis* (Elateridae) showed a higher oxygen consumption per unit of weight than larger ones. According to Edwards (*op. cit.*) an individual of 30 mg fw respires 900 mm$^3$ $O_2$ g$^{-1}$ fw h$^{-1}$ at +12°C and an individual of 45 mg fw respires about 800 mm$^3$ $O_2$ g$^{-1}$ fw h$^{-1}$ at the same

temperature. These figures were used to calculate the oxygen consumption of adult *Agriotes lineatus* L. and *A. obscurus* L. of corresponding body weights after adjustment to ambient temperatures according to a $Q_{10} = 4$.

The oxygen consumption rates of Heteroptera, adult Cantharidae, adult Coccinellidae and adult Chrysomelidae were calculated from the equation $Q = 390 \cdot W^{0.80}$ at +20°C (cf. Table 57). This equation was derived from the data on adult *Melasoma collaris* L. (Chrysomelidae) reported by Hågvar (1975) assuming the exponent $b$ to be 0.80. The rates were adjusted to other temperatures according to a $Q_{10} = 3$ between +20 and +5°C and a $Q_{10} = 4$ below +5°C.

Oxygen consumption rates of adult Curculionidae have been determined at various temperatures by Grimm (1973) and Schauermann (1973). Grimm (*op. cit.*) found seasonal differences in oxygen uptake rate at a given temperature, and the rates were generally higher during periods of reproduction and consumption. The adult curculionids at Spikbole were predominantly found in June when they were actively feeding and reproducing and, therefore, their oxygen consumption rates were calculated from the corresponding data given by Grimm (*op. cit.*) and Schauermann (*op. cit.*). These data indicated higher respiration per unit weight for smaller species (e.g. *Rhynchaenus fagi* L.) than for larger ones (e.g. *Otiorrhynchus singularis* L.), and the equation $Q = 40 \cdot W^{0.70}$ at +10°C (see Table 57) seemed to approximate these data. This equation was used in calculating the oxygen consumption rates of the curculionids at Spikbole after adjustment according to a $Q_{10} = 3$ down to +5°C.

Smith (1972) estimated the relationship between oxygen consumption rate and dry body weight for the larvae of *Operophthera brumata* (L.), *Hydriomena furcata* (Thunb.), *Erannis* spp. and *Cosmia trapezina* (L.). The common relationship between the oxygen consumption and the live body weight for these lepidopterans were $Q = 290 \cdot W^{0.7665}$ at +15°C when expressed in a form similar to the equations for the other above-ground arthropods (cf. Table 57). This equation was used in calculating the rates of Lepidoptera larvae, Symphyta larvae and Symphyta pupae at Spikbole, the rate of each taxon being based on the mean live body weight at each sampling. The oxygen consumption rates were adjusted to other temperatures using a $Q_{10} = 4$, which is in agreement with the results obtained by Axelsson *et al.* (1975) for *Operophthera brumata* larvae between +5 and +15°C.

Resting adults of *Drosophila, Simulium* and *Aedes* have been shown to respire 4000–6000 $mm^3$ $O_2$ $g^{-1}$ fw $h^{-1}$ at 17–25°C (Hocking, 1953). According to these figures the oxygen consumption rate at +25°C was assumed to be 5000 $m^3$ $O_2$ $g^{-1}$ fw $h^{-1}$ for the adult Diptera at Spikbole. This rate was adjusted to other temperatures according to a $Q_{10} = 3$ down to +5°C and $Q_{10} = 4$ below +5°C. The former $Q_{10}$ value is in agreement with that of adult *Phormia regina* determined by Keister & Buck (1961) for the temperature range between +6 and +25°C.

## RESULTS

The above-ground arthropods obtained by hand sorting or Tullgren funnel extraction were numerically dominated by sap-feeding insects such as Thysanoptera, Cicadina and Aphidina whose annual mean abundances were 720 (*s.e.* = 170), 120 (*s.e.* = 13) and 94 (*s.e.* = 90) individuals $m^{-2}$, respectively (Table 58). Occasionally juvenile Heteroptera (in May) and adult Sciaridae (in October) showed abundances higher than 100 $m^{-2}$, while other taxa were less numerous.

The biomass of the above-ground arthropods was dominated by large and medium-sized forms occurring in relatively small numbers. High biomasses were obtained for Lepidoptera larvae with 88 (*s.e.* = 88) mg dw $m^{-2}$ in October and 230 (*s.e.* = 230) mg dw $m^{-2}$ in November, but these values are very uncertain since they were based on only one (October) and two (November) individuals in the samples (Table 57). Other high biomasses were recorded for adult *Coccinella septempunctata* L. with 110 (*s.e.* = 35) mg dw $m^{-2}$ in September, Symphyta larvae with 87 (*s.e.* = 38) mg dw $m^{-2}$ also in September and adult *Phyllobius viridicollis* L. with 73 (*s.e.* = 26) mg dw $m^{-2}$ in June.

High oxygen consumption rates were calculated for *P. viridicollis* and *Agriotes lineatus* in June, for Aphidina, Symphyta and *C. septempunctata* in September and for Lepidoptera in October and November (Table 60). The annual respiration was 1.3 (*s.e.* = 0.75) kcal $m^{-2}$ for Coleoptera, 0.73 (*s.e.* = 0.27) kcal $m^{-2}$ for Lepidoptera larvae, 0.72 (*s.e.* = 0.70) kcal $m^{-2}$ for Aphidina and 0.70 (*s.e.* = 0.37) kcal $m^{-2}$ for Symphyta larvae, which were the four taxa with the highest contribution to the annual respiration.

## DISCUSSION

The arthropods were the dominant above-ground animals at Spikbole. Hares, moose, roe deer and different birds were occasionally observed on the research plot, but their production of faeces and carcasses to the soil system was probably negligible in comparison with that of the arthropods. The only vertebrate of quantitative significance on the research plot was the water vole, *Arvicola terrestris* L. The water vole was, however, in a population low in 1971–72 and, furthermore, must be considered to belong to the soil fauna. The rejecta and carcasses from the above-ground arthropods were, therefore, considered to approximate the total input to the soil from the above-ground fauna.

Separation into feeding habits revealed that the above-ground herbivores were much more abundant than the above-ground carnivores. The herbivores, which according to the classification here included Thysanoptera, Cicadina, Aphidina, *Stygnocoris, Drymus, Agriotes, Chrysomela, Chaetocnema, Phyllobius, Brachysomus, Lixus, Ceuthorrhynchus,* Symphyta, Lepidoptera and Diptera, amounted to about 1000 individuals $m^{-2}$ on an annual basis, while the carnivores amounted to 33 (*s.e.* = 21) $m^{-2}$. The classification of adult Diptera as a herbivorous group is not totally correct (adult Ceratopogonidae are, for example, carnivorous), but since the Diptera species were pooled as regards biomass and respiration, it was preferred to put the whole taxon into one feeding category. According to this classification the annual mean biomass of the herbivores was 125 (*s.e.* =

Table 58. Abundance (no. $m^{-2}$) of above-ground arthropods in 1971–72. "Summer" and annual means are based on only four "summer" samplings for some taxa. Standard error is given within parentheses below the corresponding mean value.
n.e. = not estimated (but considered as equal to the corresponding "summer" mean in estimating the May totals)
ad = adults juv = juveniles l = larvae p = pupae
T = Tullgren funnel extraction H = Hand sorting

| | | | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|---|
| Thysanoptera, total | | (T) | n.e. | 622 (235) | 399 (101) | 1495 (798) | 798 (291) | 828 (237) | 503 (134) | 720 (164) |
| Cicadina, total | | (T) | n.e. | 117 (25) | 202 (52) | 138 (67) | 138 (58) | 149 (19) | 63 (13) | 120 (13) |
| Aphidina, total | | (T) | n.e. | 0 | 543 (178) | 11 (11) | 11 (7.1) | 141 (134) | 0 | 94 (90) |
| *Picromerus bidens* | ad | (H) | 0 | 0 | 1.1 (1.1) | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *Stygnocoris pedestris* | ad | (H) | 0 | 0 | 2.1 (1.5) | 0 | 0 | 0.4 (0.4) | 0 | 0.3 (0.3) |
| *Drymus ryei* | ad | (H) | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 (0.5) | 0.2 (0.2) |
| *Nabis flavomarginatus* | ad | (H) | 0 | 0 | 2.1 (1.5) | 0 | 0 | 0.4 (0.4) | 0 | 0.3 (0.3) |
| *N. brevis* | ad | (H) | 0 | 1.1 (1.1) | 4.3 (2.5) | 3.2 (2.4) | 1.1 (1.1) | 1.9 (0.8) | 0 | 1.3 (0.6) |
| Heteroptera sp. | juv | (T) | n.e. | 159.6 (54.4) | 0 | 0 | 0 | 39.9 (39.9) | 0 | 26.6 (26.6) |
| Heteroptera, total | | (T + H) | 40 | 161 | 9.6 | 3.2 | 1.1 | 43 (31) | 0.5 (0.5) | 29 (21) |
| *Cantharis nigricans* | ad | (H) | 0 | 1.1 (1.1) | 0 | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *Agriotes lineatus* | ad | (H) | 0 | 2.1 (2.1) | 0 | 0 | 0 | 0.4 (0.4) | 0 | 0.3 (0.3) |
| *A. obscurus* | ad | (H) | 0 | 0 | 1.1 (1.1) | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *Coccidula rufa* | ad | (H) | 0 | 1.1 (1.1) | 4.3 (2.5) | 1.1 (1.1) | 0 | 1.3 (0.8) | 0.5 (0.5) | 1.0 (0.6) |
| *Scymnus redtenbacheri* | ad | (T + H) | 0 | 5.3 (5.3) | 0 | 10.6 (7.1) | 0 | 3.2 (2.2) | 0 | 2.1 (1.5) |
| *Coccinella septempunctata* | ad | (H) | 0 | 0 | 11.7 (3.7) | 0 | 0 | 2.4 (2.4) | 0 | 1.6 (1.6) |
| *Chrysomela staphylea* | ad | (H) | 0 | 0 | 0 | 1.1 (1.1) | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *Chaetocnema sahlbergi* | ad | (H) | 0 | 1.1 (1.1) | 0 | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *Phyllobius piri* | ad | (H) | 0 | 7.5 (2.7) | 0 | 0 | 0 | 1.5 (1.5) | 0 | 1.0 (1.0) |
| *P. viridicollis* | ad | (H) | 0 | 60.8 (21.4) | 0 | 0 | 0 | 12.2 (12.2) | 0 | 8.1 (8.1) |
| *Brachysomus echinatus* | ad | (H) | 1.1 (1.1) | 0 | 0 | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *Lixus iridis* | ad | (H) | 0 | 0 | 1.1 (1.1) | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| *Ceuthorrhynchus punctiger* | ad | (H) | 0 | 1.1 (1.1) | 0 | 1.1 (1.1) | 0 | 0.4 (0.3) | 0 | 0.3 (0.2) |
| Coleoptera, total | ad | (H) | 1.1 | 80 | 18 | 14 | 0 | 23 (15) | 0.5 (0.5) | 15 (9.9) |
| Symphyta, total | l | (H) | 1.1 (1.1) | 2.1 (1.5) | 6.4 (2.1) | 1.1 (1.1) | 0 | 2.1 (1.2) | 0 | 1.4 (0.8) |
| Symphyta, total | p | (H) | 0 | 0 | 1.1 (1.1) | 0 | 0 | 0.2 (0.2) | 0 | 0.1 (0.1) |
| Lepidoptera, total | l | (H) | 1.1 (1.1) | 1.1 (1.1) | 3.2 (1.8) | 1.1 (1.1) | 3.2 (1.8) | 1.9 (0.6) | 0.5 (0.5) | 1.5 (0.4) |
| Psychodidae sp. | ad | (T) | n.e. | 0 | 5.3 (5.3) | 0 | 0 | 1.3 (1.3) | 0 | 0.9 (0.9) |
| Ceratopogonidae sp. | ad | (T) | n.e. | 0 | 5.3 (5.3) | 5.3 (5.3) | 5.3 (5.3) | 4.0 (1.4) | 0 | 2.7 (0.9) |
| Sciaridae sp. | ad | (T) | n.e. | 16.0 (11.4) | 16.0 (8.2) | 122.3 (23.9) | 90.4 (21.1) | 61.2 (27.0) | 1.8 (1.8) | 41.4 (18.0) |
| Cecidomyiidae sp. | ad | (T) | n.e. | 10.6 (7.1) | 5.3 (5.3) | 0 | 0 | 4.0 (2.6) | 0 | 2.7 (1.7) |
| *Anthomyza cingulata* | ad | (T) | n.e. | 0 | 5.3 (5.3) | 0 | 0 | 1.3 (1.3) | 0 | 0.9 (0.9) |
| *Stiphrosoma sabulosum* | ad | (T) | n.e. | 31.9 (14.2) | 0 | 0 | 0 | 8.0 (3.6) | 0 | 5.3 (2.4) |
| *Pseudocollinella septentrionalis* | ad | (T) | n.e. | 0 | 0 | 5.3 (5.3) | 0 | 1.3 (1.3) | 0 | 0.9 (0.9) |
| *Oscinella cariciphila* | ad | (T) | n.e. | 0 | 5.3 (5.3) | 0 | 0 | 1.3 (1.3) | 0 | 0.9 (0.9) |
| Diptera, total | ad | (T) | n.e. | 59 (22) | 43 (16) | 133 (29) | 96 (23) | 82 (21) | 1.8 (1.8) | 56 (14) |
| A.–g. arthropods, total | | (T + H) | 1244 | 1042 | 1225 | 1796 | 1047 | 1271 (138) | 569 (139) | 1037 (103) |

Table 59. Biomass (mg dry weight $m^{-2}$) of above-ground arthropods in 1971–72. "Summer" and annual means are based on only four "summer" samplings for some taxa. Standard error is given within parentheses below the corresponding mean value.
n.e. = not estimated (but considered as equal to the corresponding "summer" mean in estimating the May totals)
ad = adults juv = juveniles l = larvae p = pupae

| | | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|---|
| Thysanoptera, total | | n.e. | 2.5 (1.0) | 1.6 (0.4) | 6.0 (3.2) | 3.2 (1.2) | 3.3 (1.0) | 2.0 (0.6) | 2.9 (0.7) |
| Cicadina, total | | n.e. | 12 (2.5) | 20 (5.2) | 14 (6.7) | 14 (5.8) | 15 (1.9) | 6.3 (1.3) | 12 (1.3) |
| Aphidina, total | | n.e. | 0 | 27 (8.9) | 0.5 (0.5) | 0.5 (0.4) | 7.1 (6.7) | 0 | 4.7 (4.5) |
| *Picromerus bidens* | ad | 0 | 0 | 26.6 (26.6) | 0 | 0 | 5.3 (5.3) | 0 | 3.5 (3.5) |
| *Stygnocoris pedestris* | ad | 0 | 0 | 1.1 (0.9) | 0 | 0 | 0.2 (0.2) | 0 | 0.2 (0.2) |
| *Drymus ryei* | ad | 0 | 0 | 0 | 0 | 0 | 0 | 0.5 (0.5) | 0.2 (0.2) |
| *Nabis flavomarginatus* | ad | 0 | 0 | 19.3 (13.4) | 0 | 0 | 3.9 (3.9) | 0 | 2.6 (2.6) |
| *N. brevis* | ad | 0 | 2.0 (2.0) | 13.2 (7.5) | 10.4 (7.6) | 2.5 (2.5) | 5.6 (2.6) | 0 | 3.8 (1.8) |
| Heteroptera sp. | juv | n.e. | 16.0 (5.5) | 0 | 0 | 0 | 4.0 (4.0) | 0 | 2.7 (2.7) |
| Heteroptera, total | | 4.0 | 18 | 60 | 10 | 2.5 | 19 (11) | 0.5 (0.5) | 13 (7.1) |
| *Cantharis nigricans* | ad | 0 | 6.2 (6.2) | 0 | 0 | 0 | 1.2 (1.2) | 0 | 0.8 (0.8) |
| *Agriotes lineatus* | ad | 0 | 21.6 (21.6) | 0 | 0 | 0 | 4.3 (4.3) | 0 | 2.9 (2.9) |
| *A. obscurus* | ad | 0 | 0 | 15.5 (15.5) | 0 | 0 | 3.1 (3.1) | 0 | 2.1 (2.1) |
| *Coccidula rufa* | ad | 0 | 0.8 (0.8) | 5.5 (3.3) | 0.8 (0.8) | 0 | 1.4 (1.1) | 0.7 (0.7) | 1.2 (0.8) |
| *Scymnus redtenbacheri* | ad | 0 | 1.4 (1.4) | 0 | 2.8 (1.9) | 0 | 0.8 (0.6) | 0 | 0.6 (0.4) |
| *Coccinella septempunctata* | ad | 0 | 0 | 107.6 (34.8) | 0 | 0 | 21.5 (21.5) | 0 | 14.3 (14.3) |
| *Chrysomela staphylea* | ad | 0 | 0 | 0 | 5.5 (5.5) | 0 | 1.1 (1.1) | 0 | 0.7 (0.7) |
| *Chaetocnema sahlbergi* | ad | 0 | 0.5 (0.5) | 0 | 0 | 0 | 0.1 (0.1) | 0 | 0.1 (0.1) |
| *Phyllobius piri* | ad | 0 | 28.0 (9.9) | 0 | 0 | 0 | 5.6 (5.6) | 0 | 3.7 (3.7) |
| *P. viridicollis* | ad | 0 | 73.0 (25.7) | 0 | 0 | 0 | 14.6 (14.6) | 0 | 9.8 (9.8) |
| *Brachysomus echinatus* | ad | 1.1 (1.1) | 0 | 0 | 0 | 0 | 0.2 (0.2) | 0 | 0.2 (0.2) |
| *Lixus iridis* | ad | 0 | 0 | 39.4 (39.4) | 0 | 0 | 7.9 (7.9) | 0 | 5.3 (5.3) |
| *Ceuthorrhynchus punctiger* | ad | 0 | 1.9 (1.9) | 0 | 1.5 (1.5) | 0 | 0.7 (0.5) | 0 | 0.5 (0.3) |
| Coleoptera, total | ad | 1.1 | 133 | 168 | 11 | 0 | 63 (37) | 0.7 (0.7) | 42 (25) |
| Symphyta, total | l | 9.6 (9.6) | 26 (18) | 87 (38) | 12 (12) | 0 | 27 (16) | 0 | 18 (11) |
| Symphyta, total | p | 0 | 0 | 17 (17) | 0 | 0 | 3.4 (3.4) | 0 | 2.3 (2.3) |
| Lepidoptera, total | l | 8.2 (8.2) | 13 (13) | 1.9 (1.2) | 88 (88) | 231 (227) | 68 (44) | 25 (25) | 54 (31) |
| Diptera, total | ad | n.e. | 5.9 (2.2) | 4.3 (1.6) | 13 (2.9) | 9.6 (2.3) | 8.2 (2.1) | 0.2 (0.2) | 5.6 (1.4) |
| A.–g. arthropods, total | | 56 | 210 | 388 | 154 | 260 | 214 (56) | 35 (26) | 154 (38) |

Table 60. Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) and annual respiration (kcal $m^{-2}$) of above-ground arthropods in 1971–72. "Summer" and annual means are based on only four "summer" samplings for some taxa. Standard error is given within parentheses below the corresponding mean value. + denotes a value less than 0.005.
n.e. = not estimated (but considered as equal to the corresponding "summer" mean in estimating the May totals)
ad = adults juv = juveniles l = larvae p = pupae

| | | Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) | | | | | | | | Annual respiration (kcal $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|---|
| | | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual | |
| Thysanoptera, total | | n.e. | 0.30 (0.12) | 0.14 (0.04) | 0.35 (0.19) | 0.11 (0.05) | 0.23 (0.06) | 0.05 (0.02) | 0.17 (0.04) | 0.30 (0.07) |
| Cicadina, total | | n.e. | 0.48 (0.11) | 0.58 (0.15) | 0.27 (0.13) | 0.17 (0.07) | 0.37 (0.10) | 0.05 (0.01) | 0.27 (0.07) | 0.47 (0.11) |
| Aphidina, total | | n.e. | 0 | 2.40 (0.79) | 0.03 (0.03) | 0.02 (0.02) | 0.61 (0.60) | 0 | 0.41 (0.40) | 0.72 (0.70) |
| *Picromerus bidens* | ad | 0 | 0 | 0.32 (0.32) | 0 | 0 | 0.06 (0.06) | 0 | 0.04 (0.04) | 0.08 (0.08) |
| *Stygnocoris pedestris* | ad | 0 | 0 | 0.03 (0.03) | 0 | 0 | 0.01 (0.01) | 0 | + | 0.01 (0.01) |
| *Drymus ryei* | ad | 0 | 0 | 0 | 0 | 0 | 0 | + | + | + |
| *Nabis flavomarginatus* | ad | 0 | 0 | 0.29 (0.20) | 0 | 0 | 0.06 (0.06) | 0 | 0.04 (0.04) | 0.07 (0.07) |
| *N. brevis* | ad | 0 | 0.05 (0.05) | 0.24 (0.14) | 0.14 (0.11) | 0.02 (0.02) | 0.09 (0.05) | 0 | 0.06 (0.03) | 0.11 (0.06) |
| Heteroptera sp. | juv | n.e. | 0.78 (0.27) | 0 | 0 | 0 | 0.20 (0.20) | 0 | 0.13 (0.13) | 0.23 (0.23) |
| Heteroptera, total | | 0.20 | 0.84 | 0.89 | 0.14 | 0.02 | 0.42 (0.19) | + | 0.28 (0.13) | 0.49 (0.22) |
| *Cantharis nigricans* | ad | 0 | 0.13 (0.13) | 0 | 0 | 0 | 0.03 (0.03) | 0 | 0.02 (0.02) | 0.03 (0.03) |
| *Agriotes lineatus* | ad | 0 | 1.11 (1.11) | 0 | 0 | 0 | 0.22 (0.22) | 0 | 0.15 (0.15) | 0.26 (0.26) |
| *A. obscurus* | ad | 0 | 0 | 0.49 (0.49) | 0 | 0 | 0.10 (0.10) | 0 | 0.07 (0.07) | 0.11 (0.11) |
| *Coccidula rufa* | ad | 0 | 0.03 (0.03) | 0.12 (0.08) | 0.01 (0.01) | 0 | 0.03 (0.03) | + | 0.02 (0.02) | 0.04 (0.03) |
| *Scymnus redtenbacheri* | ad | 0 | 0.06 (0.06) | 0 | 0.06 (0.05) | 0 | 0.02 (0.02) | 0 | 0.02 (0.01) | 0.03 (0.02) |
| *Coccinella septempunctata* | ad | 0 | 0 | 1.60 (0.52) | 0 | 0 | 0.32 (0.32) | 0 | 0.21 (0.21) | 0.38 (0.38) |
| *Chrysomela staphylea* | ad | 0 | 0 | 0 | 0.07 (0.07) | 0 | 0.01 (0.01) | 0 | 0.01 (0.01) | 0.02 (0.02) |
| *Chaetocnema sahlbergi* | ad | 0 | 0.02 (0.02) | 0 | 0 | 0 | + | 0 | + | + |
| *Phyllobius piri* | ad | 0 | 0.32 (0.12) | 0 | 0 | 0 | 0.06 (0.06) | 0 | 0.04 (0.04) | 0.08 (0.08) |
| *P. viridicollis* | ad | 0 | 1.17 (0.42) | 0 | 0 | 0 | 0.23 (0.23) | 0 | 0.16 (0.16) | 0.28 (0.28) |
| *Brachysomus echinatus* | ad | 0.02 (0.02) | 0 | 0 | 0 | 0 | + | 0 | + | + |
| *Lixus iridis* | ad | 0 | 0 | 0.17 (0.17) | 0 | 0 | 0.03 (0.03) | 0 | 0.02 (0.02) | 0.04 (0.04) |
| *Ceuthorrhynchus punctiger* | ad | 0 | 0.03 (0.03) | 0 | 0.01 (0.01) | 0 | 0.01 (0.01) | 0 | 0.01 (0.01) | 0.01 (0.01) |
| Coleoptera, total | ad | 0.02 | 2.86 | 2.39 | 0.16 | 0 | 1.09 (0.64) | + | 0.73 (0.43) | 1.27 (0.75) |
| Symphyta, total | l | 0.30 (0.30) | 0.77 (0.53) | 1.74 (0.75) | 0.17 (0.17) | 0 | 0.60 (0.32) | 0 | 0.40 (0.21) | 0.70 (0.37) |
| Symphyta, total | p | 0 | 0 | 0.26 (0.26) | 0 | 0 | 0.05 (0.05) | 0 | 0.04 (0.04) | 0.06 (0.06) |
| Lepidoptera, total | l | 0.27 (0.27) | 0.38 (0.38) | 0.08 (0.05) | 0.79 (0.79) | 1.30 (1.28) | 0.57 (0.22) | 0.11 (0.11) | 0.41 (0.15) | 0.73 (0.27) |
| Diptera, total | ad | n.e. | 0.42 (0.16) | 0.23 (0.09) | 0.53 (0.12) | 0.23 (0.06) | 0.35 (0.08) | + | 0.24 (0.05) | 0.42 (0.09) |
| A.–g. arthropods, total | | 2.35 | 6.05 | 8.71 | 2.45 | 1.86 | 4.28 (1.34) | 0.23 (0.13) | 2.93 (0.90) | 5.15 (1.57) |

25) mg dw $m^{-2}$ which was about four times higher than that of the carnivores of 29 (*s.e.* = 22) mg dw $m^{-2}$. The herbivores respired 4.2 (*s.e.* = 1.1) kcal $m^{-2}$ $yr^{-1}$ and the carnivores 1.0 (*s.e.* = 0.6) kcal $m^{-2}$ $yr^{-1}$.

Some species have already been treated in Coleoptera (p. 95) and Acari (p. 140) although they were classified as above-ground herbivores. Thus, 10 % of the total Prostigmata were believed to be above-ground owing to the frequent occurrence of the above-ground forms Eriophyidae, Tetranychidae and *Siteroptes* sp. Furthermore, the carabids *Amara* and *Harpalus* were classified as above-ground herbivores. When these species are included in the above-ground estimates, the annual mean abundance would be 6100 (*s.e.* = 560) $m^{-2}$, the annual mean biomass would be 200 (*s.e.* = 38) mg dw $m^{-2}$, and the annual respiration would be 6.5 (*s.e.* = 1.7) kcal $m^{-2}$ $yr^{-1}$ for the total above-ground Arthropoda (cf. Tables 61–63). The corresponding estimates for the different feeding categories above-ground are given in Tables 64 and 65.

Heal & MacLean (1975) suggested that annual production, respiration and egestion for invertebrate herbivores were 16, 24 and 60 % of the annual consumption, respectively, and the corresponding figures for invertebrate carnivores were 24, 56 and 20 %. These percentages were used here in order to obtain approximate estimates of the annual consumption, egestion and production of the different feeding categories at Spikbole. Thus, the above-ground herbivore respiration of 5.5 kcal $m^{-2}$ $yr^{-1}$ corresponds to a consumption of 22.9 kcal $m^{-2}$ $yr^{-1}$, an egestion of 13.7 kcal $m^{-2}$ $yr^{-1}$ and a tissue production of 3.7 kcal $m^{-2}$ $yr^{-1}$. Similarly, the above-ground carnivore respiration of 1.0 kcal $m^{-2}$ $yr^{-1}$ indicates a consumption of 1.7 kcal $m^{-2}$ $yr^{-1}$, an egestion of 0.3 kcal $m^{-2}$ $yr^{-1}$ and a tissue production of 0.4 kcal $m^{-2}$ $yr^{-1}$. Assuming that the above-ground carnivores only feed an above-ground herbivores and that no predation occurs on carnivores, 2.0 kcal $m^{-2}$ $yr^{-1}$ of the herbivore production and 0.4 kcal $m^{-2}$ $yr^{-1}$ of the carnivore production, i.e. totally 2.4 kcal $m^{-2}$ $yr^{-1}$, would reach the litter and soil as carcasses from above-ground sources. The total drop of rejecta (egesta and excreta, the latter probably energetically insignificant) would be 14.0 kcal $m^{-2}$ $yr^{-1}$ and, consequently, the total above-ground contribution of rejecta and carcasses to the below-ground saprovores would be 16.4 kcal $m^{-2}$ $yr^{-1}$ (cf. Fig. 27).

# SYNTHESIS

## INTRODUCTION

The study of the grassland ecosystem at Spikbole was focused on the energetical role of the litter- and soil-inhabiting annelids and arthropods. Interest was concentrated more on obtaining annual mean estimates of abundance, biomass and respiration of the animals than on obtaining a detailed knowledge of the population dynamics. The samplings were allocated in time according to a stratified random sampling design with a limited number of sampling occasions (cf. General methods, p. 30). Even so, the more intensive sampling during the period with unfrozen soil ("summer") still allowed some conclusions to be made on population fluctuations (cf. General discussion, p. 152). The number, biomass and respiration of the above-ground arthropods could also be estimated, since two of the four different-sized soil sample units included the vegetation (cf. Above-ground fauna, p. 159). However, sampling design and extraction technique were not optimized with regard to the above-ground fauna.

The energetical significance of the litter- and soil-inhabiting annelids and arthropods could not be evaluated without knowledge, at least in approximate terms, of the other components in the ecosystem and their contribution to the energy turnover. Therefore, it was necessary to estimate the net primary production and the plant litter production that constitute the major inputs of energy to the heterotrophic organisms.

## ABUNDANCE, BIOMASS AND RESPIRATION OF THE LARGER TAXA

The abundances of the annelids and arthropods at Spikbole were dominated by litter- and soil-dwelling forms, and the above-ground forms only accounted for about 2 % of the total number (Table 61). Acari was the numerically dominant taxon above-ground with an annual mean of about 5000 $m^{-2}$. The annual means of Thysanoptera and Homoptera were in the region of 700 $m^{-2}$ and 200 $m^{-2}$, respectively, and the other above-ground forms were considerably less frequent. The total mean number of the above-ground arthropods was about 6000 $m^{-2}$. The numbers of the below-ground anne-

Table 61. Abundance (no. $m^{-2}$) of the above- and below-ground annelids and arthropods at Spikbole in 1971–72. Litter-dwelling animals are included in the below-ground fauna. Standard error is given within parentheses below the corresponding mean value.
+ denotes a value less than 0.5.
n.e. = not estimated (but considered as equal to the corresponding "summer" mean in estimating the May totals).

| | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|
| ABOVE-GROUND FAUNA | | | | | | | | |
| Thysanoptera | n.e. | 622 | 399 | 1 495 | 798 | 828 (237) | 503 (134) | 720 (164) |
| Homoptera (part) | n.e. | 117 | 745 | 149 | 149 | 290 (152) | 63 (13) | 214 (102) |
| Heteroptera | 40 | 161 | 10 | 3 | 1 | 43 (31) | 1 (1) | 29 (20) |
| Coleoptera (part) | 12 | 85 | 21 | 15 | 1 | 27 (15) | 2 (1) | 19 (10) |
| Hymenoptera (part) | 1 | 2 | 7 | 1 | 0 | 2 (2) | 0 | 2 (1) |
| Lepidoptera | 1 | 1 | 3 | 1 | 3 | 2 (1) | 1 (1) | 1 (1) |
| Diptera (part) | n.e. | 59 | 43 | 133 | 96 | 82 (21) | 2 (2) | 56 (14) |
| Acari (part)* | 2 432 | 3 019 | 2 475 | 2 494 | 5 099 | 3 104 (511) | 8 927 (1 413) | 5 045 (581) |
| Above-ground, total | 3 687 | 4 066 | 3 704 | 4 291 | 6 147 | 4 379 (457) | 9 498 (1 395) | 6 085 (556) |
| BELOW-GROUND FAUNA | | | | | | | | |
| Enchytraeidae | 34 331 | 27 350 | 18 646 | 21 457 | 28 377 | 26 032 (2 753) | 19 413 (2 927) | 23 826 (2 079) |
| Lumbricidae | 125 | 106 | 114 | 132 | 103 | 116 (6) | 167 (29) | 133 (11) |
| Isopoda | 0 | 0 | 0 | 0 | 0 | 0 | 1 (1) | + |
| Diplopoda | 1 | 1 | 5 | 0 | 1 | 2 (1) | 2 (2) | 2 (1) |
| Symphyla | 0 | 0 | 0 | 0 | 1 | + | 0 | + |
| Collembola* | 58 704 | 49 198 | 83 231 | 54 435 | 83 214 | 65 756 (7 288) | 194 454 (32 448) | 108 655 (11 857) |
| Protura | 0 | 123 | 62 | 123 | 0 | 62 (28) | 0 | 41 (19) |
| Diplura | 0 | 0 | 0 | 0 | 0 | 0 | 74 (74) | 25 (25) |
| Blattodea | 0 | 0 | 2 | 4 | 0 | 1 (1) | 1 (1) | 1 (1) |
| Psocoptera | 62 | 62 | 123 | 0 | 0 | 49 (24) | 0 | 33 (16) |
| Homoptera (part) | 0 | 335 | 186 | 5 | 0 | 105 (68) | 4 (4) | 72 (46) |
| Coleoptera (part) | 916 | 746 | 2 179 | 1 896 | 1 454 | 1 438 (275) | 1 323 (145) | 1 400 (190) |
| Hymenoptera (part) | n.e. | 119 | 87 | 107 | 101 | 104 (7) | 113 (46) | 107 (16) |
| Diptera (part)* | 1 949 | 994 | 12 888 | 12 002 | 2 489 | 6 064 (2 620) | 4 485 (1 145) | 5 538 (1 788) |
| Opiliones | n.e. | 5 | 0 | 0 | 0 | 1 (1) | 0 | 1 (1) |
| Araneae | n.e. | 85 | 309 | 298 | 186 | 219 (53) | 151 (37) | 197 (38) |
| Acari (part)* | 46 209 | 84 871 | 79 610 | 81 319 | 95 755 | 77 553 (8 324) | 165 553 (16 857) | 106 886 (7 898) |
| Below-ground, total | 142 620 | 163 996 | 197 443 | 171 779 | 211 681 | 177 504 (12 243) | 385 741 (45 505) | 246 916 (17 225) |

*indicates that the "summer" values of these taxa are probably underestimates (cf. General discussion)

lids and arthropods were dominated by the microarthropods Collembola and Acari. Together they accounted for 87 % of the total annual mean of 247 000 (*s.e.* = 18 000) $m^{-2}$ of the below-ground forms (Table 61). Also Enchytraeidae, Diptera (larvae and pupae) and Coleoptera showed annual mean densities of more than 1000 $m^{-2}$, while other taxa were less frequent.

The seasonal fluctuation in density of the below-ground totals (Table 61) closely reflects the abundances of Collembola and Acari owing to their numerical dominance. The additional August sampling, not presented in Table 61, showed an abundance of 240 000 $m^{-2}$ of Collembola and Acari. With regard to the underestimation during the "summer" period (cf. General discussion, p. 145) this figure indicates that Collembola and Acari and, hence, the total Annelida and Arthropoda had a peak abundance in mid- and late summer (cf. Fig. 25). The low May estimate indicates a density low in the late spring.

The above-ground arthropods accounted for less than 2 % of the total annelid and arthropod biomass at Spikbole (Table 62). Coleoptera, Lepidoptera and Hymenoptera Symphyta dominated the annual mean above-ground biomass of 0.20 (*s.e.* = 0.04) g dw $m^{-2}$, while the abundant groups Acari and Thysanoptera made a very small contribution to this estimate. The annual mean below-ground biomass was dominated by Lumbricidae (about 6 g dw $m^{-2}$) and Coleoptera (about 3 g dw $m^{-2}$). Also Enchytraeidae (0.85 g dw $m^{-2}$) and Diptera (0.65 g dw $m^{-2}$) contributed significantly to the total below-ground biomass, whose annual mean was estimated at 10.6 (*s.e.* = 0.75) g dw $m^{-2}$ (Table 62).

The seasonal fluctuation in biomass of most below-ground annelid and arthropod taxa showed a minimum during the summer and a maximum during the autumn. This was evident for Coleoptera, owing to the dominance of *Phyllobius piri*, and for Diptera (Table 62), but also Enchytraeidae, Acari and Collembola showed a similar pattern (cf. Figs. 24 and 25). The small seasonal fluctuations in the biomass of Lumbricidae moderated the fluctuations in the total below-ground biomass, which was found to be lowest in June and highest in October. However, the occurrence of large Diptera pupae at the June sampling indicated that the absolute summer minimum below-ground was reached somewhat later, i.e. after the pupal hatching and emergence of imagines. In contrast to the below-ground biomass the above-ground biomass was very low during the "winter". The above-ground biomass was highest at the September sampling, but the lack of data during the mid-summer period makes a thorough analysis of the biomass fluctuations impossible, especially since the above-ground fauna was also influenced by migration to and from the adjacent forest edges.

The annual respiration of the above-ground arthropods was estimated at 6.5 (*s.e.* = 1.7) kcal $m^{-2}$ $yr^{-1}$ which was about 3 % of the total annelid and arthropod respiration (Table 63). The below-ground annelids and arthropods respired 200 (*s.e.* = 25) kcal $m^{-2}$ $yr^{-1}$. The respiration of the below-ground forms was dominated by Lumbricidae with 75 kcal $m^{-2}$ $yr^{-1}$, but because of the low respiration rates per unit weight this dominance was less pronounced than indicated by the large dominance in biomass. Also Enchytraeidae (42 kcal $m^{-2}$ $yr^{-1}$), Coleoptera (42 kcal $m^{-2}$ $yr^{-1}$) and Diptera (30 kcal $m^{-2}$ $yr^{-1}$) contributed significantly to the total annelid and arthropod respiration. The total respiration of the below-ground annelids and arthropods fluctuated seasonally mainly according to the soil temperature, but due to the low biomass during the middle of the summer the respiration did not reach its maximum during this period despite high temperatures.

Table 62. Biomass (mg dry weight $m^{-2}$) of the above- and below-ground annelids and arthropods at Spikbole in 1971–72. Litter-dwelling animals are included in the below-ground fauna. Standard error is given within parentheses below the corresponding mean value.
+ denotes a value less than 0.5.
n.e. = not estimated (but considered as equal to the corresponding "summer" mean in estimating the May totals).

| | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual |
|---|---|---|---|---|---|---|---|---|
| ABOVE-GROUND FAUNA | | | | | | | | |
| Thysanoptera | n.e. | 2 | 2 | 6 | 3 | 3 (1) | 2 (1) | 3 (1) |
| Homoptera (part) | n.e. | 12 | 47 | 14 | 14 | 22 (9) | 6 (2) | 17 (6) |
| Heteroptera | 4 | 18 | 60 | 10 | 3 | 19 (11) | + | 13 (8) |
| Coleoptera (part) | 112 | 186 | 250 | 27 | 50 | 125 (42) | 11 (6) | 87 (28) |
| Hymenoptera (part) | 10 | 26 | 104 | 12 | 0 | 30 (19) | 0 | 20 (13) |
| Lepidoptera | 8 | 13 | 2 | 88 | 231 | 68 (44) | 25 (25) | 54 (31) |
| Diptera (part) | n.e. | 6 | 4 | 13 | 10 | 8 (3) | + | 6 (2) |
| Acari (part)* | 1 | 1 | 1 | 1 | 1 | 1 (1) | 3 (1) | 1 (1) |
| Above-ground, total | 168 | 264 | 470 | 171 | 312 | 277 (56) | 47 (26) | 200 (38) |
| BELOW-GROUND FAUNA | | | | | | | | |
| Enchytraeidae | 870 | 556 | 536 | 1 075 | 997 | 807 (112) | 942 (182) | 852 (90) |
| Lumbricidae | 6 386 | 6 071 | 6 059 | 7 108 | 5 736 | 6 272 (233) | 5 252 (1 287) | 5 932 (456) |
| Isopoda | 0 | 0 | 0 | 0 | 0 | 0 | 12 (12) | 4 (4) |
| Diplopoda | 34 | 34 | 1 | 0 | 14 | 17 (8) | 54 (43) | 29 (16) |
| Symphyla | 0 | 0 | 0 | 0 | + | + | 0 | + |
| Collembola* | 138 | 69 | 99 | 86 | 131 | 105 (14) | 217 (28) | 142 (13) |
| Protura | 0 | + | + | + | 0 | + | 0 | + |
| Diplura | 0 | 0 | 0 | 0 | 0 | 0 | + | + |
| Blattodea | 0 | 0 | 1 | 5 | 0 | 1 (1) | 3 (3) | 2 (2) |
| Psocoptera | + | + | + | 0 | 0 | + | 0 | + |
| Homoptera (part) | 0 | 2 | 1 | + | 0 | 1 (1) | + | + |
| Coleoptera (part) | 2 725 | 563 | 4 009 | 3 481 | 2 971 | 2 750 (590) | 2 933 (427) | 2 811 (418) |
| Hymenoptera (part) | 3 | 4 | 6 | 4 | 2 | 4 (1) | 6 (3) | 4 (1) |
| Diptera (part)* | 823 | 226 | 330 | 1 407 | 637 | 685 (210) | 589 (106) | 653 (145) |
| Opiliones | n.e. | + | 0 | 0 | 0 | + | 0 | + |
| Araneae | n.e. | 50 | 43 | 55 | 53 | 50 (3) | 17 (6) | 39 (3) |
| Acari (part)* | 93 | 88 | 129 | 150 | 116 | 115 (12) | 156 (10) | 129 (9) |
| Below-ground, total | 11 123 | 7 663 | 11 213 | 13 370 | 10 657 | 10 805 (915) | 10 183 (1 301) | 10 598 (749) |

*indicates that the "summer" values of these taxa are probably underestimates (cf. General discussion)

Table 63. Oxygen consumption rates and annual respiration of the above- and below-ground annelids and arthropods at Spikbole in 1971–72. Litter-dwelling animals are included in the below-ground fauna. Standard error is given within parantheses below the corresponding mean value.
+ denotes a value less than 0.05.
n.e. = not estimated (but considered as equal to the corresponding "summer" mean in estimating the May totals).

| | Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) | | | | | | | | Annual respiration | |
|---|---|---|---|---|---|---|---|---|---|---|
| | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual | (kcal $m^{-2}$) | (kJ $m^{-2}$) |
| ABOVE-GROUND FAUNA | | | | | | | | | | |
| Thysanoptera | n.e. | 0.3 | 0.1 | 0.4 | 0.1 | 0.2 (0.1) | 0.1 (0.1) | 0.2 (0.1) | 0.3 (0.1) | 1.2 (0.3) |
| Homoptera (part) | n.e. | 0.5 | 3.0 | 0.3 | 0.2 | 1.0 (0.7) | 0.1 (0.1) | 0.7 (0.5) | 1.2 (0.8) | 5.0 (3.3) |
| Heteroptera | 0.2 | 0.8 | 0.9 | 0.1 | + | 0.4 (0.2) | + | 0.3 (0.2) | 0.5 (0.3) | 2.1 (0.9) |
| Coleoptera (part) | 2.2 | 4.0 | 3.6 | 0.4 | 0.4 | 2.1 (0.8) | 0.1 (0.1) | 1.4 (0.5) | 2.5 (0.9) | 10.6 (3.7) |
| Hymenoptera (part) | 0.3 | 0.8 | 2.0 | 0.2 | 0 | 0.6 (0.4) | 0 | 0.4 (0.3) | 0.8 (0.5) | 3.2 (1.8) |
| Lepidoptera | 0.3 | 0.4 | 0.1 | 0.8 | 1.3 | 0.6 (0.3) | 0.1 (0.1) | 0.4 (0.2) | 0.7 (0.3) | 3.0 (1.1) |
| Diptera (part) | n.e. | 0.4 | 0.2 | 0.5 | 0.2 | 0.4 (0.1) | + | 0.2 (0.1) | 0.4 (0.1) | 1.7 (0.4) |
| Acari (part) | + | + | + | + | + | + | + | + | + | 0.2 (0.1) |
| Above-ground, total | 4.6 | 7.2 | 9.9 | 2.7 | 2.3 | 5.3 (1.5) | 0.3 (0.2) | 3.7 (1.0) | 6.5 (1.7) | 27.0 (7.1) |
| BELOW-GROUND FAUNA | | | | | | | | | | |
| Enchytraeidae | 41.6 | 28.7 | 22.2 | 34.3 | 22.8 | 29.9 (3.7) | 12.4 (2.4) | 24.1 (2.6) | 42.3 (4.6) | 177.1 (18.9) |
| Lumbricidae | 71.0 | 55.8 | 56.8 | 57.3 | 30.4 | 54.3 (6.6) | 19.8 (4.6) | 42.8 (4.7) | 75.2 (8.2) | 314.5 (34.1) |
| Isopoda | 0 | 0 | 0 | 0 | 0 | 0 | + | + | + | 0.1 (0.1) |
| Diplopoda | 0.1 | 0.1 | + | 0 | + | + | + | + | 0.1 (0.1) | 0.2 (0.1) |
| Symphyla | 0 | 0 | 0 | 0 | + | + | 0 | + | + | + |
| Collembola | 5.0 | 3.3 | 4.0 | 2.4 | 2.4 | 3.4 (0.5) | 3.6 (0.5) | 3.5 (0.4) | 6.1 (0.7) | 25.5 (2.7) |
| Protura | 0 | + | + | + | 0 | + | 0 | + | + | + |
| Diplura | 0 | 0 | 0 | 0 | 0 | 0 | + | + | + | + |
| Blattodea | 0 | 0 | + | 0.2 | 0 | + | + | + | 0.1 (0.1) | 0.3 (0.2) |
| Psocoptera | + | + | + | 0 | 0 | + | 0 | + | + | + |
| Homoptera (part) | 0 | 0.1 | + | + | 0 | + | + | + | + | 0.1 (0.1) |
| Coleoptera (part) | 32.9 | 10.1 | 70.7 | 24.5 | 14.7 | 30.6 (10.8) | 9.8 (0.9) | 23.7 (7.2) | 41.6 (12.7) | 173.9 (52.9) |
| Hymenoptera (part) | 0.1 | 0.1 | 0.1 | 0.1 | + | 0.1 (0.1) | + | 0.1 (0.1) | 0.1 (0.1) | 0.4 (0.1) |
| Diptera (part) | 34.4 | 9.0 | 14.2 | 45.3 | 8.6 | 22.3 (7.5) | 7.1 (1.2) | 17.3 (5.0) | 30.3 (8.8) | 126.8 (36.6) |
| Opiliones | n.e. | + | 0 | 0 | 0 | + | 0 | + | + | + |
| Araneae | n.e. | 0.6 | 0.5 | 0.5 | 0.3 | 0.5 (0.1) | 0.1 (0.1) | 0.4 (0.1) | 0.6 (0.1) | 2.6 (0.3) |
| Acari (part) | 2.1 | 2.3 | 2.2 | 1.9 | 1.0 | 1.9 (0.3) | 1.2 (0.1) | 1.7 (0.2) | 2.9 (0.3) | 12.1 (1.2) |
| Below-ground, total | 187.7 | 110.1 | 170.8 | 166.4 | 80.4 | 143.1 (20.4) | 54.1 (6.2) | 113.4 (13.8) | 199.3 (24.2) | 833.7 (101.1) |

The standard errors originating from the sampling procedure were relatively low (7–11 % of the annual means) for the abundance, biomass and respiration of Enchytraeidae, Lumbricidae, Collembola and Acari. The standard errors for these characteristics of below-ground Coleoptera and Diptera were 14–32 % of the annual means, thus reflecting the more pronounced fluctuations during the year. The corresponding standard errors for the total below-ground annelids and arthropods were 7, 7 and 12 % for the abundance, biomass and respiration, respectively. A conclusion that can be drawn from these figures, i.e. the standard errors being about 10 % of the annual means, is that a real difference between the means cannot be detected ($P < 0.05$) unless the estimated means diverge more than expressed by the ratio 2:3. This demonstrates the difficulty in ascertaining small and moderate differences in soil fauna populations, e.g. between sites or successional stages, without very extensive sampling.

## BIOMASS AND RESPIRATION OF DIFFERENT FEEDING CATEGORIES

The above- and below-ground annelids and arthropods at Spikbole were separated into five broad feeding categories, above-ground herbivores, above-ground carnivores, below-ground herbivores, below-ground carnivores and saprovores/microbivores. The classification into different feeding habits was sometimes difficult owing to lack of data in the literature and sometimes hazardous owing to omnivorous habits of the animals. The reason for each classification has been given in the taxonomic presentations.

The saprovores/microbivores dominated the total biomass of the annelids and arthropods on all sampling occasions, and their annual mean biomass of 7.5 (*s.e.* = 0.6) g dw $m^{-2}$ was considerably higher than those of the below-ground herbivores and carnivores (Table 64). The above-ground herbivores had a much higher annual biomass than the above-ground carnivores. The biomass fluctuations were less pronounced for the below-ground carnivores and the saprovores/microbivores than for the other three categories. The energy equivalents of the annual mean biomasses of the different feeding categories are also given in Table 64. The saprovores/microbivores, who dominated the annelid and arthropod respiration accounted for 150 (*s.e.* = 19) kcal $m^{-2}$ $yr^{-1}$ of the total respiration of 206 (*s.e.* = 25) kcal $m^{-2}$ $yr^{-1}$ (Table 65).

## RELATIVE CONTRIBUTION TO BIOMASS AND RESPIRATION

The relative contribution to biomass and respiration provides a first basis in evaluating the energetical significance of the soil animals. The contribution by the below-ground annelids and arthropods at Spikbole was analyzed with regard to species, larger taxa and feeding categories (Fig. 26). The ten dominant species accounted for 89 % of the annual

Table 64. Biomass (g dry weight $m^{-2}$) of different feeding categories of annelids and arthropods at Spikbole in 1971 - 72. The energy equivalent of the annual mean biomass (kcal $m^{-2}$) is also given. Standard error is given within parentheses below the corresponding mean value.
+ denotes a value less than 0.005.

| | Biomass (g dry weight $m^{-2}$) | | | | | | | | Annual mean energy content (*) (kcal $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|
| | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual | |
| Above-ground herbivores | 0.16 | 0.24 | 0.30 | 0.16 | 0.31 | 0.23 (0.04) | 0.05 (0.03) | 0.17 (0.03) | 0.94 (0.13) |
| Above-ground carnivores | + | 0.03 | 0.17 | 0.01 | + | 0.04 (0.04) | + | 0.03 (0.03) | 0.17 (0.13) |
| Below-ground herbivores | 2.47 | 0.41 | 3.65 | 3.17 | 2.67 | 2.47 (0.56) | 2.70 (0.43) | 2.55 (0.40) | 14.02 (2.19) |
| Below-ground carnivores | 0.59 | 0.39 | 0.60 | 0.60 | 0.65 | 0.56 (0.05) | 0.50 (0.07) | 0.54 (0.04) | 3.14 (0.22) |
| Saprovores/microbivores | 8.05 | 6.87 | 6.97 | 9.60 | 7.35 | 7.77 (0.51) | 6.99 (1.27) | 7.51 (0.54) | 37.54 (2.70) |
| **Total** | 11.29 | 7.93 | 11.68 | 13.54 | 10.97 | 11.08 (0.91) | 10.23 (1.30) | 10.80 (0.75) | 55.81 (3.88) |

(*) The calorific equivalents are generalized to be 5.0 kcal $g^{-1}$ for saprovores/microbivores, 5.5 kcal $g^{-1}$ for herbivores and 5.8 kcal $g^{-1}$ for carnivores (cf. Bolton, 1969; Edwards *et al.*, 1970; Smith, 1972; Axelsson *et al.*, 1973a; Naess *et al.*, 1975; Wallwork, 1975).

Table 65. Oxygen consumption rates and annual respiration of different feeding categories of annelids and arthropods at Spikbole in 1971–72. Standard error is given within parentheses below the corresponding mean value.
+ denotes a value less than 0.05.

| | Oxygen consumption rates ($cm^3$ $O_2$ $m^{-2}$ $day^{-1}$) | | | | | | | | Annual respiration | |
|---|---|---|---|---|---|---|---|---|---|---|
| | May 17 | June 15 | Sept 13 | Oct 28 | Nov 11 | "Summer" | "Winter" | Annual | (kcal $m^{-2}$) | (kJ $m^{-2}$) |
| Above-ground herbivores | 4.4 | 6.1 | 7.3 | 2.5 | 2.3 | 4.5 (1.0) | 0.3 (0.2) | 3.1 (0.1) | 5.5 (1.2) | 23.0 (4.9) |
| Above-ground carnivores | 0.2 | 1.1 | 2.6 | 0.2 | + | 0.8 (0.5) | + | 0.5 (0.4) | 1.0 (0.6) | 4.0 (2.4) |
| Below-ground herbivores | 26.0 | 4.1 | 58.4 | 13.4 | 7.2 | 21.8 (9.9) | 5.8 (0.8) | 16.5 (6.6) | 28.9 (11.6) | 121.0 (48.5) |
| Below-ground carnivores | 16.6 | 12.2 | 17.0 | 15.5 | 11.0 | 14.5 (1.3) | 6.4 (0.8) | 11.8 (0.9) | 20.7 (1.5) | 86.4 (6.3) |
| Saprovores/microbivores | 145.1 | 93.9 | 95.3 | 137.5 | 62.2 | 106.8 (15.4) | 42.0 (5.4) | 85.2 (10.4) | 149.7 (18.3) | 626.2 (76.2) |
| **Total** | 192.3 | 117.3 | 180.7 | 169.1 | 82.7 | 148.4 (20.9) | 54.5 (5.6) | 117.1 (14.1) | 205.7 (24.7) | 860.7 (103.0) |

mean biomass while their contribution to the annual respiration was lower, 77 %. Thus, the remaining 240 species (or more) contributed 11 % to the annual mean biomass and 23 % to the annual respiration. Consequently, more species had a significant influence on the annual respiration than on the annual mean biomass.

Lumbricidae, Coleoptera, Enchytraeidae and Diptera dominated the biomass and respiration of the annelids and arthropods in the soil. The contributions to the annual respiration were much more evenly distributed between these four taxa than the contributions to the annual mean biomass, where Lumbricidae alone accounted for 56 %. The annelids (Lumbricidae and Enchytraeidae) dominated over the arthropods both as regards the biomass (64 %) and the respiration (59 %). The macroarthropods (Coleoptera,

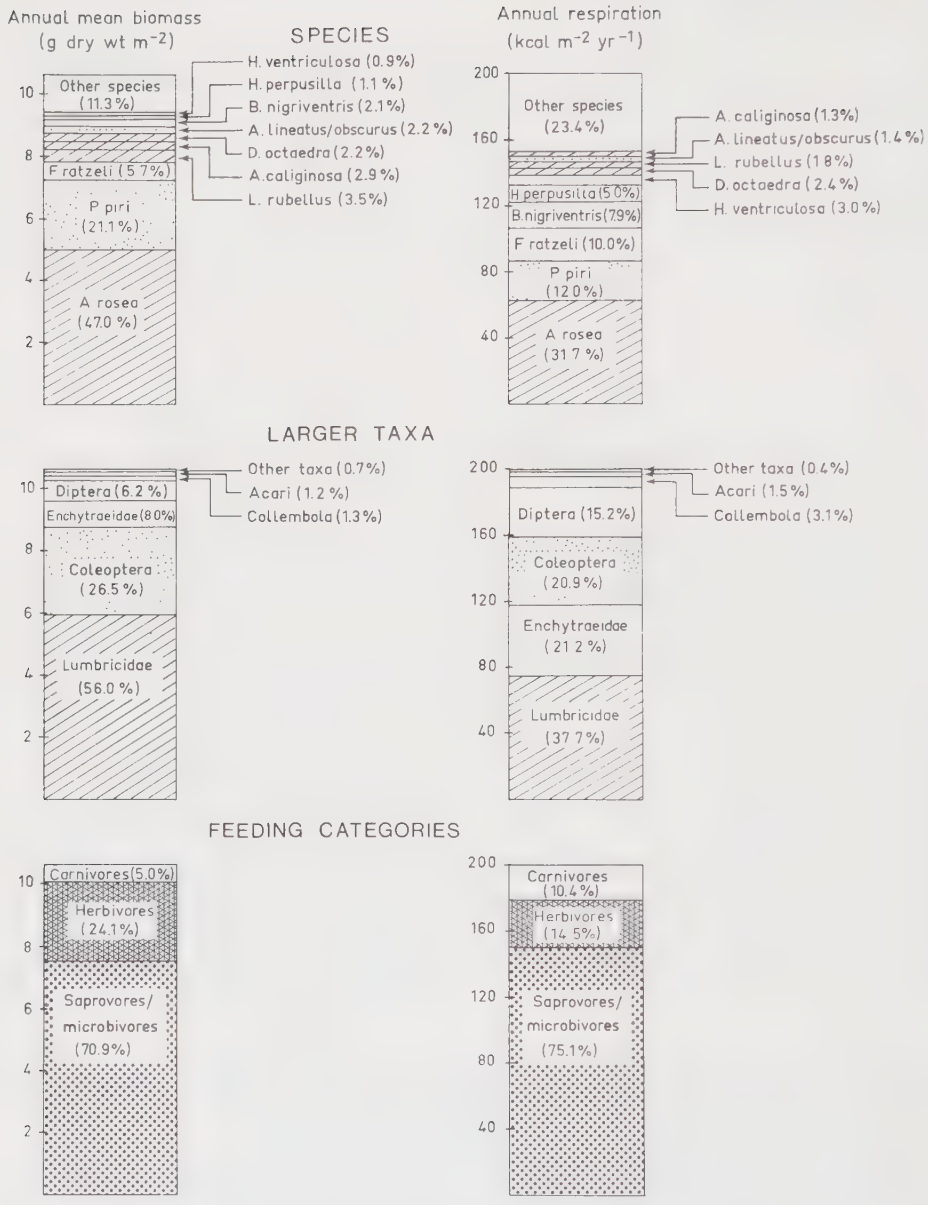


**Figure 26.** Contribution by individual species, larger taxa and feeding categories to the annual mean biomass (10.6 g dw $m^{-2}$) and the annual respiration (200 kcal $m^{-2}$ $yr^{-1}$) of the below-ground annelid and arthropod community at Spikbole during 1971–72.

Diptera, Diplopoda and Araneae, among others) surpassed the microarthropods (Collembola and Acari) both concerning biomass (33.5 % and 2.5 %, respectively) and respiration (36.3 % and 4.6 %, respectively). The small contribution by Collembola and Acari to the biomass and respiration may look remarkable in view of some earlier investigations, but it is probable that the mean weights of, for example, Collembola have been overestimated by many researchers (e.g. Macfadyen, 1963; Kitazawa, 1971). Furthermore, the microarthropod fauna at Spikbole was dominated by very small forms.

The litter- and soil-inhabiting annelids and arthropods were dominated by the saprovores/microbivores both as regards the annual mean biomass (71 %) and the annual respiration (75 %) (Fig. 26). The herbivores contributed proportionally more to the biomass (24 %) than to the respiration (15 %), while the carnivores showed a greater contribution to the respiration (10 %) than to the biomass (5 %). The relationship between respiration ($R$) and the energy stored in the biomass ($B$) gives a measure of the metabolic activity per unit weight. The $R/B$ ratios on an annual basis were 2.1 for the below-ground herbivores, 4.0 for the saprovores/microbivores and 6.6 for the below-ground carnivores (cf. Tables 64 and 65). These ratios can hardly be used for generalizations, since they are largely dependent on site-specific characters such as taxonomic composition, size composition and course of biomass fluctuation. The latter factor can be exemplified by the herbivore *P. piri* that had a life cycle with a high biomass during periods of low temperature which, consequently, caused low respiration rates during that time and a low $R/B$ ratio on an annual basis.

## ENERGY FLOW THROUGH THE ECOSYSTEM

The relationships between flows and storages of energy or material in an ecosystem are often well conceptualized in a flow chart. The data obtained at Spikbole were summarized in an energy flow diagram (Fig. 27) of the same structure as in Fig. 1. The storages were represented by the energy equivalents of the annual mean biomasses and the annual means of dead matter, and the flows were also given on an annual energy basis. For the sake of entirety it was necessary to guess the annual mean biomass and the annual respiration of soil animals not belonging to the annelids and arthropods. The amounts of dead plant matter, rejecta and carcasses, and dead and alive microorganisms were not estimated separately and could not be quantified in the diagram. Energy flows in the form of animal migration were neglected in Fig. 27 assuming that the migration to and from the research plot balanced each other.

### Solar energy and primary producers

The global radiation (300–3000 nm) in 1971 was 834 000 kcal $m^{-2}$ which constituted the input of solar energy to the photosynthetic plants. Since only about 45 % of the radiant energy is available to the vegetation owing to the spectral composition (Anderson, 1967; Moir, 1969) and since the growing season, here defined as the period during which the mean temperature at the soil surface is higher than +3°C (Ångström,

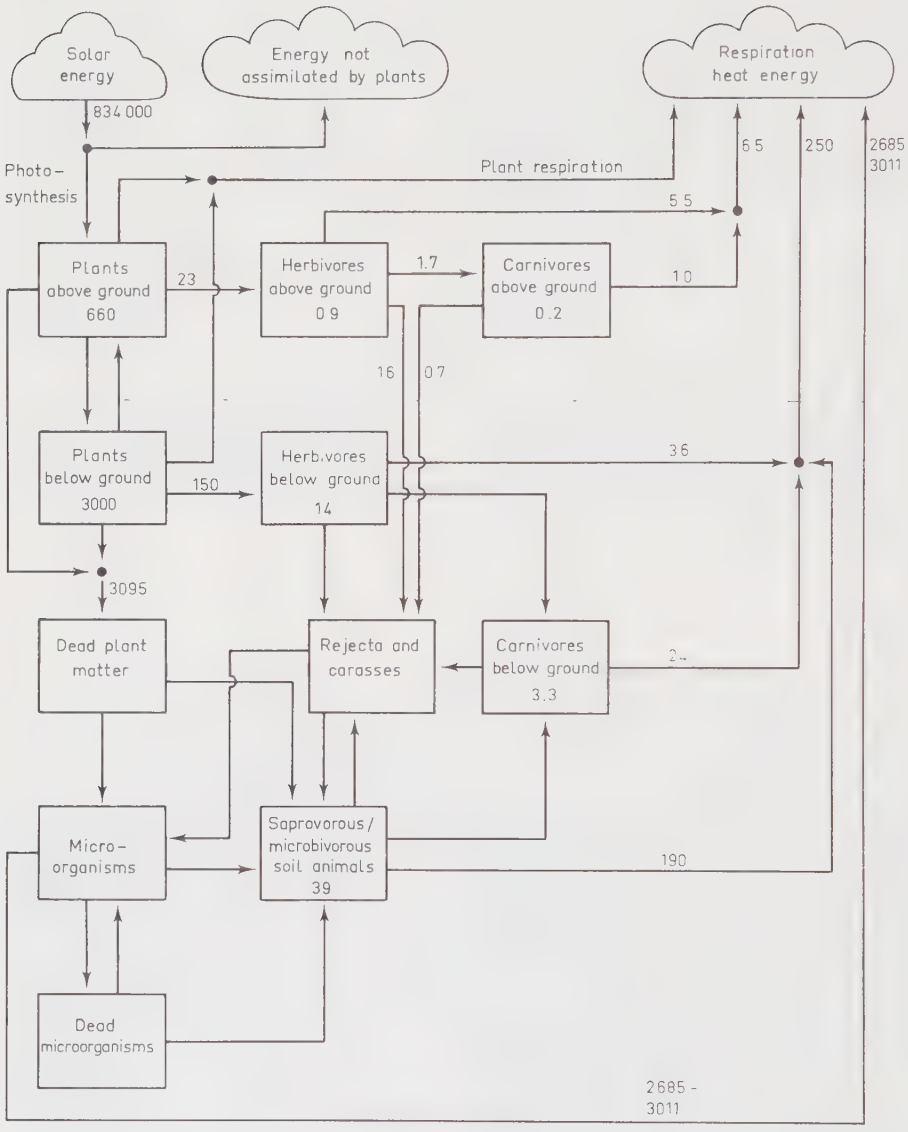


**Figure 27.** Energy flow diagram of the grassland ecosystem at Spikbole during 1971–72. Storages (kcal $m^{-2}$) and flows (kcal $m^{-2}$ $yr^{-1}$) quantified in the diagram are estimated or derived from studies at Spikbole. The broken line defines the boundary between above- and below-ground. For further explanation see Fig. 1.

1958), only lasted 180 days in 1971 (May 2 to October 28), the solar energy available to the plants at Spikbole was 294 000 kcal $m^{-2}$ during this period.

Part of the solar energy was assimilated by the primary producers that were dominated by perennial grasses. The peak above-ground plant biomass in 1971 was slightly more than 400 g dw $m^{-2}$. The annual mean above-ground plant biomass was estimated at about 150 g dw $m^{-2}$ which was equivalent to about 660 kcal $m^{-2}$. The biomass of the below-ground fractions produced in 1971 was about 280 g dw $m^{-2}$ for the dominant species, *Agropyron repens*, and about 320 g dw $m^{-2}$ for the whole plant community. The total below-ground biomass was not estimated, but assuming an annual turnover of 40 % for the below-ground parts (cf. Dahlman, 1968; Nilsson, 1970) the energy equivalent of the annual mean biomass would be in the region of 3000 kcal $m^{-2}$.

The net primary production (NPP) excluding herbivore consumption for the plant community at Spikbole was estimated at 2654 kcal $m^{-2}$ in 1971. The consumption by the above-ground herbivores was indirectly estimated at 23 kcal $m^{-2}$ $yr^{-1}$ (see below), and the consumption by the below-ground herbivores was estimated at 150 kcal $m^{-2}$ $yr^{-1}$ (see also below). The total NPP was, thus, 2827 kcal $m^{-2}$ $yr^{-1}$ or 0.96 % of the available solar energy. The total NPP in 1971 was not equal to the litter production during the same period, since the litter production from the perennial roots and rhizomes was dependent on the preceding years' NPP. Therefore, the plant litter production in 1971 was calculated as the mean of the NPP values less herbivore consumption in 1969–71, i.e. 3095 kcal $m^{-2}$ $yr^{-1}$ (cf. Primary producers, p. 27).

## Above-ground fauna

The above-ground fauna at Spikbole was undoubtedly dominated by the arthropods whose annual mean biomass (Table 64) and annual respiration (Table 65) were inserted in Fig. 27. The above-ground herbivore respiration of 5.5 kcal $m^{-2}$ $yr^{-1}$ corresponds to a consumption of 22.9 kcal $m^{-2}$ $yr^{-1}$, and the above-ground carnivore respiration of 1.0 kcal $m^{-2}$ $yr^{-1}$ corresponds to a consumption of 1.7 kcal $m^{-2}$ $yr^{-1}$ according to the efficiency quotients suggested by Heal & MacLean (1975). According to these quotients the output of energy in the form of rejecta and carcasses would be 15.7 kcal $m^{-2}$ $yr^{-1}$ from the above-ground herbivores and 0.7 kcal $m^{-2}$ $yr^{-1}$ from the above-ground carnivores (cf. Above-ground fauna, p. 166, and Fig. 27). These figures indicate that the above-ground herbivore consumption accounted for a removal of 0.8 % of the NPP. About 0.2 % of the NPP was released as respiration energy and 0.6 % reached the soil system.

## Below-ground fauna

The annual mean biomasses and annual respiration figures of the below-ground annelids and arthropods, given in Tables 62–65, only account for a part, although certainly the dominant part, of the total below-ground fauna. The fauna also consisted of Protozoa, Nematoda, Rotatoria, Tardigrada and Mollusca. The contribution of these taxa to the annual mean biomass and annual respiration of the soil fauna was not estimated, but in order to make the energy flow diagram (Fig. 27) more complete it was necessary to make some additional guesses. Assuming an annual mean number of 5 000 000 $m^{-2}$ and an annual mean biomass of 250 mg dw $m^{-2}$ of Nematoda (cf. Nielsen, 1949;

Banage, 1963; Wasilewska, 1974) the annual respiration of this taxon would be 35 kcal $m^{-2}$ $yr^{-1}$ according to data by Klekowski *et al.* (1972) and after temperature correction ($Q_{10}$ = 2 above +5°C and $Q_{10}$ = 4 below +5°C). The annual mean biomass and annual respiration of the remaining part of the soil fauna (Protozoa, Rotatoria, Tardigrada and Mollusca) was assumed to be 150 mg dw $m^{-2}$ and 16 kcal $m^{-2}$ $yr^{-1}$, respectively, the latter value being in accordance with that given by Satchell (1971) for Protozoa and Mollusca (15 kcal $m^{-2}$ $yr^{-1}$) in a deciduous wood in England. Twenty per cent of the nematode biomass and respiration were assumed to belong to the below-ground herbivores and 10 % to the below-ground carnivores (cf. Banage, 1963; Wasilewska, 1974). The remaining 70 % of the nematodes, as well as the other taxa, were classified as saprovores/microbivores.

Using the same calorific equivalents as suggested in Fig. 64, the annual mean biomasses for the total soil fauna would be 14 kcal $m^{-2}$ for the below-ground herbivores, 3.3 kcal $m^{-2}$ for the below-ground carnivores and 39 kcal $m^{-2}$ for the saprovores/microbivores. The annual respiration figures would be 36 kcal $m^{-2}$ $yr^{-1}$ for the below-ground herbivores, 24 kcal $m^{-2}$ $yr^{-1}$ for the below-ground carnivores and 190 kcal $m^{-2}$ $yr^{-1}$ for the saprovores/microbivores (Fig. 27). These figures would imply an annual mean biomass of 11.0 g dw $m^{-2}$ for the total soil fauna compared with 10.6 g dw $m^{-2}$ for the below-ground annelids and arthropods, and an annual respiration of 250 kcal $m^{-2}$ $yr^{-1}$ for the total soil fauna compared with 200 kcal $m^{-2}$ $yr^{-1}$ for the below-ground annelids and arthropods.

The annual respiration of 36 kcal $m^{-2}$ $yr^{-1}$ of the below-ground herbivores corresponds to a consumption of 150 kcal $m^{-2}$ $yr^{-1}$ according to the efficiency quotients given by Heal & MacLean (1975). This consumption is equivalent to a removal of 5.3 % of the NPP in 1971. Since the above-ground herbivores ingested 0.8 % of the NPP, the total herbivore consumption accounted for a removal of 6.1 % of the NPP in 1971.

## Heterotrophic soil respiration

The total energy input to the below-ground heterotrophs during the actual study period was estimated as the sum of plant litter production (3095 kcal $m^{-2}$ $yr^{-1}$) in 1971, below-ground herbivore consumption (150 kcal $m^{-2}$ $yr^{-1}$) in 1971–72 and rejecta and carcasses from the above-ground herbivores (15.7 kcal $m^{-2}$ $yr^{-1}$) and the above-ground carnivores (0.7 kcal $m^{-2}$ $yr^{-1}$) in 1971–72, i.e. a total input of 3261 kcal $m^{-2}$ $yr^{-1}$. If no accumulation or reduction of organic matter occurred, this input was counterbalanced by an output of respiration energy of equal size. Cultivation of peat land generally causes a reduction of the organic content but since permanent leys on peat soils seem to maintain the organic content (Djurle, 1946), it was assumed that the abandoned field situation at Spikbole with a high litter production would result in a slight accumulation of the soil organic matter. An accumulation of 0–10 % of the input of organic matter to the soil system would imply a total heterotrophic soil respiration of 2935–3261 kcal $m^{-2}$ $yr^{-1}$. The annual respiration of 250 kcal $m^{-2}$ $yr^{-1}$ by the soil fauna would in that case account for 7.7–8.5 % of the heterotrophic respiration in the litter and soil, and the microorganism respiration would, consequently, account for 91.5–92.3 % or 2685–3011 kcal $m^{-2}$ $yr^{-1}$ (Fig. 27).

## ANIMAL CONTRIBUTION TO THE HETEROTROPHIC SOIL RESPIRATION

The contribution by the whole soil fauna to the total heterotrophic soil respiration has been estimated by few investigators. Satchell (1971) estimated this contribution to be about 17 % in a mixed deciduous wood in England, Andrews *et al.* (1974) found a soil animal respiration of 1.4 % both in ungrazed and a heavily grazed shortgrass prairie in Colorado, and Ryszkowski (1975) reported corresponding figures of about 4 % in cultivated fields in Poland. Other authors have related the soil animal respiration to the annual litter supply, with is normally not directly equivalent to the heterotrophic soil respiration (see above), but often not far from it. The annual respiration by the soil fauna in relation to the litter supply was estimated at about 10–20 % in various European ecosystems (Macfadyen, 1963), 1.4–8.1 % in early succession stages on brown coal dumps in Germany (Dunger, 1968), 0.9–9 % in a series from alpine to tropical forests (Kitazawa, 1971) and 0.8–5.2 % in Finnish spruce stands (Huhta & Koskenniemi, 1975). Furthermore, the contribution to the total invertebrate respiration (dominated by below-ground forms) to the net primary production was 21 % for a limestone grassland, 23 % for an alluvial grassland, 6 % for a *Juncus* moor and 3 % for a blanket bog in an upland area (Moor House) in England (Coulson & Whittaker, in press).

The animal contribution of about 8 % to the annual heterotrophic soil respiration at Spikbole thus seems to be of the same order of magnitude as that in many other terrestrial ecosystems investigated. However, the estimates are not directly comparable owing to different methods and more or less rough approximations. Nevertheless, they support the common conclusion that the release of energy by the soil animals is far lower than that by the microorganisms.

## SIGNIFICANCE OF THE ANNELIDS AND ARTHROPODS IN THE SOIL

The annelid and arthropod respiration of 200 (*s.e.* = 25) kcal $m^{-2}$ $yr^{-1}$ contributed 6–7 % to the heterotrophic soil respiration at Spikbole. In a way this contribution expresses the energetical significance of the annelids and arthropods in relation to the whole heterotrophic community in the soil since besides being a direct measure of energy release, respiration is also a measure of the metabolic activity. The annual respiration figures given for individual species, larger taxa, feeding categories and the whole annelid and arthropod fauna can, therefore, serve as indexes for evaluating the participation in the overall activity in the soil. However, respiration must not be considered as the only measure of energetical importance, since the metabolic activity is also reflected by consumption, egestion and production of tissues, among others, On an annual basis these transfers of energy seem to be closely related to respiration and can be approximately calculated by means of efficiency quotients (Reichle, 1971; Heal & MacLean, 1975). According to Heal & MacLean's (*op. cit.*) efficiency quotients for invertebrates, saprovores have low assimilation efficiencies ($A/C$), microbivores and herbivores have moder-

ate ones and carnivores have high ones. These quotients mean that the respiration of 29 kcal $m^{-2}$ $yr^{-1}$ for the below-ground herbivores within Annelida and Arthropoda would correspond to a tissue production of 19, an egestion of 72 and a consumption of 120 kcal $m^{-2}$ $yr^{-1}$. The respiration of 150 kcal $m^{-2}$ $yr^{-1}$ for the saprovores/microbivores would correspond to a production of 100, an egestion of 750 and a consumption of 1000 kcal $m^{-2}$ $yr^{-1}$. Similarly, the respiration of 21 kcal $m^{-2}$ $yr^{-1}$ for the below-ground carnivores would correspond to a production of 9, an egestion of 7 and a consumption of 37 kcal $m^{-2}$ $yr^{-1}$.

The microorganisms respired 2685–3011 kcal $m^{-2}$ $yr^{-1}$ (Fig. 27). Assuming a production efficiency ($P/A$) of 0.3 for the microorganisms (cf. Andrews *et al.*, 1974; Heal & MacLean, 1975) their annual production would amount to 1200–1300 kcal $m^{-2}$ $yr^{-1}$. The microbial feeders were not separated from the saprovorous animals in the present study but, assuming that half of the saprovore/microbivore respiration originated from microbivores, the microbivores belonging to Annelida and Arthropoda would have consumed 420 kcal $m^{-2}$ $yr^{-1}$. This consumption, although excluding non-annelid and non-arthropod consumption, constitutes a very significant withdrawal of energy from the microbial production and implies a marked influence on the microbial populations.

The herbivore and saprovore/microbivore production (within Annelida and Arthropoda) totally amounted to 119 kcal $m^{-2}$ $yr^{-1}$ according to the efficiency quotients used. This production constituted the possible input to the carnivores that, according to the consumption estimate of 37 kcal $m^{-2}$ $yr^{-1}$, ingested about a third of the available energy. However, this high rate of predation on the herbivores and saprovores/microbivores is probably an overestimate, since the top carnivores (e.g. adult Gamasina predating juvenile Gamasina and Hymenoptera Parasitica infesting carnivorous Diptera larvae) were not separated from the other carnivores as a unique category. Nevertheless, the below-ground herbivores and saprovores/microbivores were subjected to a high predation pressure, especially since the consumption value is always an underestimate of the withdrawal of energy from the prey populations as the killed prey animals are not entirely ingested by the predators.

Efficiency quotients for feeding categories provide a useful aid for an overall understanding of the interrelations between groups of organisms and trophic levels, but they are, of course, generalizations that are not very suitable for predicting bioenergetical rates of individual species that in one way or another diverge from the average type. This is exemplified with the dominant species at Spikbole as regards biomass and respiration, *Allolobophora rosea*. According to recent studies by Bolton & Phillipson (1976) *A. rosea* has a very low assimilation efficiency ($A/C$ about 0.01 in energy units) and has different $P/R$ ratios for different size classes. The data by Bolton & Phillipson (*op. cit.*) imply that the annual respiration of 63 kcal $m^{-2}$ $yr^{-1}$ of *A. rosea* at Spikbole was equivalent to a production of 21 kcal $m^{-2}$ $yr^{-1}$, an egestion of 8716 kcal $m^{-2}$ $yr^{-1}$ and a consumption of 8800 kcal $m^{-2}$ $yr^{-1}$. This consumption corresponds to an intake of about 2 kg dw $m^{-2}$ $yr^{-1}$ of organic material. Since the organic matter less roots and rhizomes amounted to 41.5 kg dw $m^{-2}$ in the upper 40 cm of the soil profile at Spikbole, the high annual consumption means that it would only take 21 years for *A. rosea* to ingest this quantity. The very high consumption rate of *A. rosea* is, if correct, about 15 times higher than calculated for an average saprovore according to the efficiency quotients given by Heal & MacLean (1975), and 10–30 times higher than calculated for

some other lumbricid species than *A. rosea* according to Crossley *et al.* (1971).

The example with *A. rosea*, which eats its way through the soil (Bolton & Phillipson, 1976), touches upon the qualitative importance of the soil animals. Respiration is only a quantitative measure of metabolic activity and does not tell us how the activity is performed. However, different species often show well-defined abilities and have different niches in the ecosystem. Hence, if we had sufficient knowledge of a species' qualitative traits we could use the annual respiration of that population as an index of activity and predict its influence on its environment, including other populations, in quantitative terms. Thus, we believe that the annual respiration estimated for individual species can be used as a key for further insight into the quantitative significance of the animals and, together with a thorough knowledge of the autecology of at least the dominant species, it will provide a fundamental means of obtaining a better understanding of the quantitative role of the soil animals.

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# Appendix 1

## PILOT STUDIES

### Introduction

During 1969 and 1970 pilot studies were made to gain knowledge of the composition and distribution of the soil fauna at Spikbole, and to prepare suitable methods of sample design, extraction technique and treatment of material. The pilot studies mainly concerned Enchytraeidae, Lumbricidae and Collembola, which were assumed to be energetically important groups in the area. Different samplings were made to assess their abundance and, in some cases, biomass.

### Methods

The samplings were made on 2 and 14 October 1969 and on 11, 21 and 26 May 1970. A stratified sampling design was used in the October samplings, when the research plot was divided into four strata of equal size in each of which two positions were chosen at random with the aid of a coordinate grid and a table with random numbers. The October estimates did not show any distinct gradient within the plot (however, see General methods, p. 30), and a simple random sampling was used at the May samplings.

The enchytraeids were sampled on 2 and 14 October 1969 and 21 and 26 May 1970. The enchytraeid soil cores were taken to variable depths (Table A 1) and the surface area of the cores were 33.2 $cm^2$ in October and 22.1 $cm^2$ in May. The enchytraeids were extracted by means of a modified Baermann funnel technique (O'Connor, 1962). The dry weights were determined at the first May sampling after weighing to the nearest 0.01 mg.

The lumbricids were sampled on 2 and 14 October 1969, when the soil cores were taken to a depth of 25 cm. The surface area was 625 $cm^2$. The lumbricids were sorted by hand in the laboratory, after which they were rinsed in water, killed by immersion for five minutes in 6 % formalin, identified to species and dried at +60°C in a vacuum drier. The dry weights including gut content were determined for each sampling.

The microarthropod sampling was carried out on 2 and 14 October and on 11 and 21 May 1970. The soil cores were taken to a depth of 20 cm except for the sampling on May 11, when the depth was only 6 cm. The surface area was 10.8 $cm^2$. The microarthropods were extracted in a high gradient canister extractor described in General meth-

ods, p. 32. The collembolans were identified and counted on each occasion, while other soil animals such as Acari, Coleoptera and Diptera larvae, which were also extracted from the microarthropod soil cores, were taken into consideration only on May 21.

## Results and discussion

The abundance and biomass of Enchytraeidae are given in Table A 1. The difference between the abundances on May 21 and May 26 was not significant, but since enchytraeids were found between the 10 and 16 cm level in the soil profile on the latter sampling occasion, it was concluded that the sample depth was insufficient on May 21 for estimating the whole enchytraeid population.

**Table A 1. Abundance (no. $m^{-2}$) and biomass (g dry weight $m^{-2}$) of Enchytraeidae in 1969 and 1970.**
**n.e. = not estimated**

| Date | Depth of soil core (cm) | no. $m^{-2}$ $\bar{x}$ | s.e. | g $m^{-2}$ $\bar{x}$ | s.e. |
|---|---|---|---|---|---|
| 1969 | | | | | |
| October 2 | 12 | 22 000 | 4 500 | n.e. | |
| October 14 | 12 | 29 300 | 10 200 | n.e. | |
| 1970 | | | | | |
| May 21 | 10 | 19 000 | 3 200 | 1.58 | 0.25 |
| May 26 | 16 | 24 700 | 4 500 | n.e. | |

The estimates of abundance and biomass of Lumbricidae in October 1969 showed that *Allolobophora rosea* was the dominant species with regard to both abundance and biomass (Table A 2). The biomasses were probably overestimated as a consequence of the gut content being included. However, *A. rosea* loses dry weight when placed in formalin because of mucus production, which counteracts the extra weight due to gut content (cf. Lumbricidae, p. 47).

The abundances of Collembola in 1969 and 1970 are presented in Table A 3, which also shows the abundances of Coleoptera (adults and larvae of Staphylinidae), Diptera larvae and Acari. *Tullbergia krausbaueri* was the numerically dominant collembolan with abundances around 50 000 $m^{-2}$. Other dominant species were *Folsomia quadrioculata* with abundances of about 10 000 $m^{-2}$, *Isotomiella minor* and *Isotoma notabilis*. The differences between the estimated mean values of the Collembola totals were not significant. As a very rough estimate, the samplings indicated an abundance of about 80 000 collembolans $m^{-2}$ both in October and in May. The number of Acari on May 21 was about half this estimate. A majority of the Diptera larvae belonged to the Nematocera group.

The experience gained in the pilot studies was used when planning the main study.

Table A 2. Abundance (no. $m^{-2}$) and biomass (g dry weight $m^{-2}$) of Lumbricidae in October 1969. The biomasses include gut content.

| | October 2 | | | | October 14 | | | |
|---|---|---|---|---|---|---|---|---|
| | no. $m^{-2}$ | | g $m^{-2}$ | | no. $m^{-2}$ | | g $m^{-2}$ | |
| | $\bar{x}$ | s.e. | $\bar{x}$ | s.e. | $\bar{x}$ | s.e. | $\bar{x}$ | s.e. |
| *Allolobophora caliginosa* | 2.0 | 2.0 | 0.13 | 0.13 | 2.0 | 2.0 | 0.17 | 0.17 |
| *A. rosea* | 80.0 | 30.4 | 3.49 | 0.24 | 52.0 | 17.2 | 2.03 | 0.58 |
| *Dendrobaena octaedra* | 20.0 | 6.4 | 0.40 | 0.20 | 28.0 | 7.0 | 0.29 | 0.09 |
| *Lumbricus rubellus* | 12.0 | 2.9 | 0.84 | 0.45 | 16.0 | 4.9 | 0.41 | 0.23 |
| Lumbricidae, total | 114.0 | 35.5 | 4.85 | 0.56 | 98.0 | 20.7 | 2.89 | 0.40 |

Table A 3. Abundance (no. $m^{-2}$) of Collembola, Acari, Coleoptera and Diptera larvae during the pilot studies in 1969 and 1970. The depths of the soil cores are indicated.
n.e. = not estimated

| Core depth (cm): | 2 October 1969 20 | | 14 October 1969 20 | | 11 May 1970 6 | | 21 May 1970 20 | |
|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | s.e. | $\bar{x}$ | s.e. | $\bar{x}$ | s.e. | $\bar{x}$ | s.e. |
| *Hypogastrura denticulata* | 3 500 | 2 300 | 690 | 590 | 1 900 | 680 | 580 | 250 |
| *Friesea mirabilis* | 120 | 120 | 0 | | 560 | 430 | 0 | |
| *Anurida pygmaea* | 120 | 120 | 120 | 120 | 90 | 90 | 120 | 120 |
| *Onychiurus armatus* | 350 | 350 | 0 | | 370 | 230 | 0 | |
| *Tullbergia krausbaueri* | 55 100 | 29 200 | 45 800 | 8 300 | 63 100 | 11 300 | 51 000 | 18 600 |
| *T. quadrispina* | 1 300 | 910 | 0 | | 880 | 740 | 0 | |
| *Folsomia quadrioculata* | 9 600 | 3 100 | 10 900 | 5 700 | 11 600 | 3 600 | 9 300 | 2 400 |
| *F. fimetaria* coll. | 3 200 | 2 000 | 2 400 | 1 700 | 2 400 | 970 | 120 | 120 |
| *Isotomiella minor* | 11 500 | 2 100 | 2 500 | 370 | 4 500 | 1 500 | 2 100 | 1 300 |
| *Isotoma notabilis* | 4 900 | 2 100 | 3 200 | 2 300 | 9 600 | 3 000 | 2 400 | 1 700 |
| *I. viridis* | 350 | 260 | 350 | 260 | 510 | 170 | 120 | 120 |
| *Entomobrya nivalis* | 1 300 | 960 | 1 200 | 550 | 370 | 140 | 120 | 120 |
| *Lepidocyrtus cyaneus* | 1 500 | 580 | 930 | 620 | 190 | 90 | 350 | 170 |
| *Megalothorax minimus* | 230 | 170 | 0 | | 0 | | 0 | |
| Sminthuridae sp. | 0 | | 0 | | 230 | 100 | 230 | 160 |
| Collembola, total | 92 900 | 32 600 | 68 200 | 8 300 | 96 300 | 13 200 | 66 400 | 17 400 |
| Staphylinidae, adults | n.e. | | n.e. | | n.e. | | 230 | 230 |
| Staphylinidae, larvae | n.e. | | n.e. | | n.e. | | 580 | 460 |
| Diptera, larvae | n.e. | | n.e. | | n.e. | | 1 000 | 280 |
| Mesostigmata | n.e. | | n.e. | | n.e. | | 2 700 | 600 |
| Other Acari | n.e. | | n.e. | | n.e. | | 35 500 | 4 800 |
| Acari, total | n.e. | | n.e. | | n.e. | | 38 200 | 4 400 |

The sampling depths of Enchytraeidae were thus increased in order to obtain more reliable estimates. The surface area of 33.2 $cm^2$ of the soil cores for Enchytraeidae used in October was judged to be slightly too large under existing population densities, and a smaller area was expected to save time in the treatments of the material without a corresponding loss of precision in the estimates. The results also showed that other soil fauna groups than Enchytraeidae, Lumbricidae and Collembola occurred frequently in the soil. The population data are discussed in connection with the results obtained in the main study.

# Appendix 2

## SPECIES LIST OF ANNELIDA AND ARTHROPODA AT SPIKBOLE

The following list consists of species collected in the 50 × 100 m research plot at Spikbole. Most of the species were determined after extraction or sorting from litter and soil samples (S), but rearing in the laboratory (R), collection in emergence traps (E), sweep-netting (N) and other collection methods (C) complemented the former method. Altogether 442 annelid and arthropod species were found at the research plot, but this is certainly a large underestimation since, for example, the sweep-nettings were not very extensive.

1 = larvae, p = pupae, ad = adults

| | Collection method |
|---|---|
| **ANNELIDA** | |
| **Oligochaeta** | |
| Enchytraeidae | |
| *Henlea perpusilla* Friend | S |
| *H. ventriculosa* (Udekem) | S |
| *Fridericia bulboides* N. & C. | S |
| *F. paroniana* Issel | S |
| *F. bisetosa* (Lev.) | S |
| *F. ratzeli* (Eisen) | S |
| *Enchytraeus minutus* N. & C. | S |
| *Marionina argentea* (Mich.) | S |
| Lumbricidae | |
| *Allolobophora caliginosa* (Sav.) | S |
| *A. rosea* (Sav.) | S |
| *Dendrobaena octaedra* (Sav.) | S |
| *D. rubida* (Sav.) f. *subrubicunda* (Eisen) | S |
| *Lumbricus rubellus* Hoffm. | S |
| **ARTHROPODA** | |
| **Isopoda** | |
| Porcellionidae | |
| Porcellionidae sp. | S |

| | Collection method |
|---|---|
| **Diplopoda** | |
| Iulidae | |
| *Schizophyllum sabulosum* L. | S |
| **Symphyla** | |
| Scutigerellidae | |
| *Scutigerella* cf. *immaculata* Newp. | S |
| **Collembola** | |
| Poduridae | |
| *Hypogastrura socialis* (Uzel) | C |
| *H. denticulata* (Bagn.) | S |
| *Willemia anophthalma* Börn. | S |
| *Friesea mirabilis* (Tullb.) | S |
| *Pseudachorutes dubius* Krausb. | S |
| *Anurida pygmaea* (Börn.) | S |
| *A. ellipsoides* Stach | S |
| *A. granaria* (Nic.) | S |
| *Neanura muscorum* (Templeton) | S |
| Onychiuridae | |
| *Onychiurus armatus* (Tullb.) | S |
| *Tullbergia krausbaueri* (Börn.) | S |
| *T. quadrispina* (Börn.) | S |
| Isotomidae | |
| *Folsomia quadrioculata* (Tullb.) | S |
| *F. bisetosa* Gisin | S |
| *F. fimetaria* (L.) | S |
| *F. litsteri* Bagn. | S |
| *Isotomiella minor* (Schäff.) | S |
| *Proisotoma minuta* (Tullb.) | S |
| *Isotoma notabilis* Schäff. | S |
| *I. viridis* Bourl. | S |
| *I. violacea* Tullb. | C |
| Entomobryidae | |
| *Entomobrya nivalis* (L.) | S |
| *Lepidocyrtus cyaneus* Tullb. | S |
| *L. lignorum* (Fabr.) | S |
| *Pseudosinella alba* (Packard) | S |
| *Tomocerus flavescens* (Tullb.) | S |
| Sminthuridae | |
| *Megalothorax minimus* Willem | S |
| *Sminthurides pumilis* (Krausb.) | S |
| *Sminthurinus niger* (Lubb.) | S |
| *Bourletiella* cf. *repanda* (Ågren) | S |
| *Sminthurus nigromaculatus* Tullb. | S |
| *Dicyrtoma minuta* (Fabr.) | S |
| **Protura** | |
| Eosentomidae | |
| *Eosentomon* cf. *germanicum* Prell | S |
| **Diplura** | |
| Campodeidae | |
| *Campodea* sp. | S |

| | Collection method |
|---|---|
| **Blattodea** | |
| Blattellidae | |
| *Ectobius lapponicus* L. | S, N |
| **Orthoptera** | |
| Tettigoniidae | |
| *Metrioptera brachyptera* L. | N |
| Acrididae | |
| *Omocestus viridulus* L. | N |
| *Chorthippus albomarginatus* DeG. | N |
| *Gomphocerippus rufus* L. | N |
| **Psocoptera** | |
| Liposcelidae | |
| *Liposcelis liparus* Broadhead | S |
| **Thysanoptera** | |
| Thripidae | |
| *Limothrips denticornis* Hal. | S |
| *Anaphothrips obscurus* Müll. | S |
| *Frankliniella tenuicornis* Uzel | S |
| *Thrips validus* Uzel | S |
| *Stenothrips graminum* Uzel | S |
| Phloeothripidae | |
| *Cephalothrips monilicornis* Reut. | S |
| *Nesothrips dentipes* Reut. | S |
| **Homoptera** | |
| Cicadina | |
| Cercopidae | |
| *Lepyronia coleoptrata* (L.) | N |
| *Philaenus spumarius* (L.) | N |
| *Neophilaenus lineatus* (L.) | N |
| Euscelidae | |
| *Aphrodes bicinctus* (Schrank) | S |
| *A. flavostriatus* (Don.) | S, E |
| *Diplocolenus abdominalis* (Fabr.) | S, E, N |
| *Arthaldeus pascuellus* (Fall.) | N |
| *Streptanus marginatus* (Kbm) | N |
| *S. aemulans* (Kbm) | S |
| *Athysanus argentarius* Metcalf | N |
| *Paluda flaveola* (Boh.) | N |
| *Elymana sulphurella* (Zett.) | S, N |
| Delphacidae | |
| *Delphacodes brevipennis* (Boh.) | N |
| *Dicranotropis hamata* (Boh.) | S |
| Aphidina | |
| Aphididae | |
| *Lachnus* sp. | S |
| *Sipha* sp. | S |
| *Rhopalosiphum padi* (L.) | S |
| *Aphis* sp. | S |
| *Diuraphis (Holcaphis) calamagrostis* (Ossiann.) | S |
| *Diuraphis (Holcaphis) frequens* (Walk.) | S |
| *Cryptaphis poae* (Hardy) | S |
| Coccina | |
| Coccina sp. | S |

| | Stage | Collection method |
|---|---|---|
| **Heteroptera** | | |
| Miridae | | |
| *Polymerus unifasciatus* (Fabr.) | | N |
| *Lygus wagneri* Rem. | | N |
| *Capsus ater* (L.) | | N |
| *Stenodema calcaratum* (Fall.) | | N |
| *Halticus apterus* (L.) | | N |
| Nabidae | | |
| *Nabis brevis* Scholtz | | S |
| *N. flavomarginatus* Scholtz | | S, N |
| Reduviidae | | |
| *Coranus subapterus* DeG. | | N |
| Tingidae | | |
| *Derephysia foliacea* (Fall.) | | N |
| Lygaeidae | | |
| *Drymus ryei* Dgl. & Sc. | | S |
| *Stygnocoris pedestris* (Fall.) | | S |
| Rhopalidae | | |
| *Myrmus miriformis* (Fall.) | | N |
| Pentatomidae | | |
| *Aelia acuminata* (L.) | | N |
| *Picromerus bidens* (L.) | | S |
| **Coleoptera** | | |
| Carabidae | | |
| *Clivina fossor* L. | l, ad | S |
| *Dyschirius globosus* Hbst | l, ad | S |
| *Bembidion lampros* Hbst | ad | S |
| *B. gilvipes* Sturm | ad | S |
| *B. guttula* Fabr. | ad | S |
| *Trechus secalis* Payk. | l, ad | S |
| *T. micros* Hbst | ad | S |
| *Harpalus latus* L. | ad | S |
| *Bradycellus collaris* Payk. | ad | S |
| *Trichocellus placidus* Gyll. | ad | S |
| *Amara communis* Panz. | ad | S |
| *A. apricaria* Payk. | ad | S |
| *A. consularis* Dft. | ad | S |
| *A. aulica* Panz. | ad | S |
| *Pterostichus versicolor* Sturm | ad | S |
| *P. melanarius* Ill. | ad | S |
| *P. strenuus* Panz. | ad | S |
| *Calathus melanocephalus* L. | l, ad | S, E |
| *C. micropterus* Dft. | l | S |
| *Agonum piceum* L. | ad | S |
| *Dromius sigma* Rossi | ad | S |
| Hydrophilidae | | |
| *Megasternum boletophagum* Marsh. | l, ad | S, R, E |
| Silphidae | | |
| *Choleva angustata* Fabr. | ad | S |
| Liodidae | | |
| *Agathidium atrum* Payk. | ad | S |

| | Stage | Collection method |
|---|---|---|
| Staphylinidae | | |
| *Pycnoglypta lurida* Gyll. | ad | S |
| *Olophrum assimile* Payk. | ad | S |
| *Arpedium quadrum* Grav. | ad | S |
| *Stenus clavicornis* Scop. | ad | S |
| *S. impressus* Germ. | ad | S |
| *Stilicus rufipes* Germ. | ad | S |
| *Lathrobium punctatum* Zett. | ad | S |
| *L. geminum* Kr. | ad | S |
| *L. fulvipenne* Grav. | ad | S |
| *L. longulum* Grav. | ad | S |
| *Xantholinus linearis* Ol. | ad | S |
| *Othius melanocephalus* Grav. | ad | S |
| *O. lapidicola* Kiesw. | ad | S |
| *Philonthus varius* Gyll. | ad | S |
| *Staphylinus fuscatus* Grav. | ad | S |
| *Quedius fuliginosus* Grav. | ad | S |
| *Q. curtipennis* Bernh. | ad | S |
| *Q. picipennis* Payk. *molochinus* Grav. | ad | S |
| *Q. fulvicollis* Steph. | ad | S |
| *Q. nitipennis* Steph. | ad | S |
| *Mycetoporus splendidus* Grav. | ad | S |
| *Conosoma pedicularium* Grav. | ad | S |
| *Tachyporus nitidulus* Fabr. | ad | S |
| *T. scutellaris* Rye | ad | S |
| *T. chrysomelinus* L. | ad | S |
| *T. pulchellus* Mannh. | ad | S |
| *Tachinus rufipes* DeG. | ad | S |
| *T. rufipennis* Gyll. | ad | S |
| *T. marginellus* Fabr. | ad | S |
| *T. corticinus* Grav. | ad | S |
| *Myllaena minuta* Grav. | ad | S |
| *Schistoglossa gemina* Er. | ad | S |
| *Amischa analis* Grav. | ad | S |
| *A. cavifrons* Sharp | ad | S |
| *Sipalia circellaris* Grav. | ad | S |
| *Atheta britteni* Joy | ad | S |
| *A. gregaria* Er. | ad | S |
| *A. fungi* Grav. | ad | S |
| *Oxypoda lividipennis* Mannh. | ad | S |
| *O. longipes* Muls. & Rey | ad | S |
| *O. vicina Kr.* | ad | S |
| *O. advena* Mäkl. | ad | S |
| *O. soror* Thoms. | ad | S |
| *Aleochara brevipennis* Grav. | ad | S |
| *A. spadicea* Er. | ad | S |
| Cantharidae | | |
| *Cantharis figurata* Mannh. | ad | N |
| *C. nigricans* Müll. | ad | S, N |
| *Rhagonycha limbata* Thoms. | ad | N |
| Dasytidae | | |
| *Dolichosoma lineare* Rossi | ad | N |

| | Stage | Collection method |
|---|---|---|
| Elateridae | | |
| *Corymbites aeneus* L. | l | S |
| *Pheletes aeneoniger* DeG. | ad | N |
| *Sericus brunneus* L. | l | S |
| *Agriotes lineatus* L. | ad | S |
| *A. obscurus* L. | ad | S |
| Nitidulidae | | |
| *Meligethes aeneus* Fabr. | ad | N |
| Cucujidae | | |
| *Airaphilus elongatus* Gyll. | ad | S |
| Cryptophagidae | | |
| *Atomaria analis* Er. | ad | S |
| *A. atricapilla* Steph. | ad | S |
| Phalacridae | | |
| *Olibrus bicolor* Fabr. | ad | S |
| Lathridiidae | | |
| *Corticaria impressa* Ol. | ad | S |
| *Corticarina fuscula* Gyll. | ad | S, E |
| Coccinellidae | | |
| *Coccidula rufa* Hbst | ad | S |
| *Scymnus redtenbacheri* Muls. | ad | S |
| *Hippodamia 13-punctata* L. | ad | N |
| *Coccinella septempunctata* L. | ad | S, N |
| *Thea 22-punctata* L. | ad | N |
| *Propylaea 14-punctata* L. | ad | N |
| Mordellidae | | |
| *Anaspis* sp. | ad | S |
| Lagriidae | | |
| *Lagria hirta* L. | l, ad | S, E, N |
| Scarabaeidae | | |
| *Aphodius fimetarius* L. | ad | E |
| Chrysomelidae | | |
| *Chrysomela fastuosa* Scop. | ad | N |
| *C. staphylea* L. | ad | S |
| *Melasoma populi* L. | ad | N |
| *Phytodecta viminalis* L. | ad | N |
| *Phyllodecta vitellinae* L. | ad | N |
| *Galerucella tenella* L. | ad | N |
| *Chaetocnema sahlbergi* Gyll. | ad | S |
| Curculionidae | | |
| *Apion hookeri* Kirby | ad | S |
| *Phyllobius maculicornis* Germ. | ad | N |
| *P. piri* L. | l, p, ad | S, R, E, N |
| *P. viridicollis* Fabr. | l, p, ad | S, R, E, N |
| *Brachysomus echinatus* Bonsd. | ad | S |
| *Lixus iridis* Ol. | ad | S |
| *Ceuthorrhynchus punctiger* Gyll. | ad | S |
| **Hymenoptera** | | |
| Symphyta | | |
| Cephidae | | |
| *Calameuta filiformis* Eversm. | ad | N |

| | Stage | Collection method |
|---|---|---|
| Tenthredinidae | | |
| *Pachynematus xanthocarpus* Htg | ad | N |
| *P. ? clitellatus* Lep. | ad | N |
| *Rhogogaster fulvipes* Scop. | ad | N |
| *Tenthredopsis litterata* Geoffr. | ad | N |
| *T. nassata* L. | ad | N |
| *Athalia rosae* L. | ad | N |
| Parasitica | | |
| Ichneumonidae | | |
| Ichneumonidae sp. | ad | N |
| Braconidae | | |
| *Aphaereta* sp. | ad | S |
| Aphidiidae | | |
| Aphidiidae sp. | ad | E |
| Eurytomidae | | |
| *Tetramesa* sp. | ad | S, E |
| Mymaridae | | |
| *Arescon* sp. | ad | S |
| *Polynema* sp. | ad | E |
| *? Anaphes* sp. | ad | S |
| Aphelinidae | | |
| *Aphytis* sp. | ad | S |
| Eulophidae | | |
| Eulophidae sp. | ad | S |
| Encyrtidae | | |
| Encyrtidae sp. | ad | S |
| Pteromalidae | | |
| Pteromalidae sp. | ad | S |
| Diapriidae | | |
| *Spilomicrus basalyformis* Marsh. | ad | S |
| *S. cf. flavipes* Thoms. | ad | S |
| *Trichopria aptera* Ruthe | ad | S |
| *T. nigra* Nees | ad | S |
| *Zygota nigra* Thoms. | ad | S |
| Scelionidae | | |
| *Gryon* sp. | ad | S |
| *Trimorus* sp. | ad | S |
| Ceraphronidae | | |
| *Conostigmus* sp. | ad | S |
| *Lagynodes* sp. | ad | S |
| *Ceraphron* sp. | ad | S |
| Platygasteridae | | |
| *Amblyaspis* sp. | ad | S |
| Cynipidae | | |
| *Pezophycta* sp. | ad | S |
| Aculeata | | |
| Formicidae | | |
| *Myrmica ruginodis* Nyl. | ad | S |
| *M. scabrinodis* Nyl. | ad | S |
| *Lasius niger* L. | ad | S |
| *Formica rufa* L. | ad | E |

| | Stage | Collection method |
|---|---|---|
| **Mecoptera** | | |
| Panorpidae | | |
| *Panorpa communis* L. | ad | N |
| **Lepidoptera** | | |
| Geometridae | | |
| *Scopula immorata* L. | ad | N |
| *Ortholitha chenopodiata* L. | ad | N |
| *Cidaria* sp. | ad | N |
| Noctuidae | | |
| Noctuidae sp. | l | S |
| Arctiidae | | |
| *Lithosia lutarella* L. | ad | N |
| *Phragmatobia fuliginosa* L. | l | S |
| Sphingidae | | |
| Sphingidae sp. | l | S |
| Hesperiidae | | |
| *Augiades sylvanus* Esp. | ad | N |
| Pieridídae | | |
| *Pieris napi* L. | ad | N |
| Lycaenidae | | |
| *Heodes virgaureae* L. | ad | N |
| Nymphalididae | | |
| *Vanessa io* L. | l, ad | N |
| *V. urticae* L. | ad | N |
| *Argynnis ino* Rott. | ad | N |
| *Brenthis* sp. | ad | N |
| Satyridae | | |
| *Aphantopus hyperantus* L. | ad | N |
| *Pararge maera* L. | ad | N |
| **Diptera** | | |
| Nematocera | | |
| Tipulidae | | |
| *Tipula variipennis* Wied. | l, ad | S, R, N |
| *Limonia tripunctata* Fabr. | ad | N |
| Psychodidae | | |
| Psychodidae sp. | ad | S |
| Chironomidae | | |
| *Smittia* sp. | l | S |
| Ceratopogonidae | | |
| *Culicoides* sp. | l | S |
| Bibionidae | | |
| *Dilophus femoratus* Meig. | ad | N |
| *Bibio clavipes* Meig. | ad | S |
| *B. ferruginatus* L. | ad | S |
| *B. nigriventris* Hal. | l, ad | S, E, N |
| Scatopsidae | | |
| Scatopsidae sp. | l | S |
| Mycetophilidae | | |
| Mycetophilidae sp. | l | S |
| Sciophilinae sp. | l | S |
| Sciaridae | | |
| *Bradysia* sp. | ad | E |
| *Scaptosciara ? vivida* Winn. | ad | R |
| *Leptosciara trochanterata* Zett. | l, ad | R, E |

| | Stage | Collection method |
|---|---|---|
| Cecidomyiidae | | |
| Lestremiinae sp. | l, ad | S, E |
| Brachycera Orthorrhapha | | |
| Rhagionidae | | |
| *Symphoromyia crassicornis* Panz. | l, ad | S, R |
| Tabanidae | | |
| *Heptatoma pellucens* Fabr. | ad | N |
| *Haematopota pluvialis* L. | ad | N |
| *Hybomitra bimaculata* Macq. | ad | N |
| *Tabanus bromius* L. | l, ad | S, R |
| Therevidae | | |
| *Thereva valida* Lw | ad | N |
| Empididae | | |
| *Platypalpus infectus* Coll. | ad | N |
| *Bicellaria sulcata* Zett. | ad | N |
| *Ramphomyia spinipes* Fall. | ad | S |
| *R. tibialis* Meig. | ad | N |
| *Empis stercorea* L. | ad | N |
| *E. tesselata* Fabr. | ad | N |
| *E. livida* L. | ad | N |
| *E. nigripes* Fabr. | ad | N |
| *Hilara interstincta* Fall. | ad | N |
| *H. litorea* Fall. | ad | N |
| Dolichopodidae | | |
| *Dolichopus plumipes* Scop. | ad | N |
| *D. popularis* Wied. | ad | N |
| *D. ungulatus* L. | ad | N |
| *D. cilifemoratus* Macq. | l, ad | S, R, E, N |
| *D. brevipennis* Meig. | l, ad | S, R, E, N |
| *D. longicornis* Stann. | ad | N |
| *Chrysotus gramineus* Fall. | ad | N |
| Brachycera Cyclorrhapha | | |
| Syrphidae | | |
| *Helophilus pendulus* L. | ad | N |
| *Xylota segnis* L. | ad | N |
| *Platychirus albimanus* Fabr. | ad | N |
| *P. peltatus* Meig. | ad | N |
| *P. angustatus* Zett. | ad | N |
| *P. clypeatus* Meig. | ad | N |
| *Melanostoma mellinum* L. | ad | N |
| *Sphaerophoria menthastri* L. | l, ad | S, R, N |
| *S. scripta* L. | ad | N |
| *Syrphus nitens* Zett. | ad | N |
| *S. balteatus* DeG. | ad | N |
| *S. vitripennis* Meig. | ad | N |
| *S. corollae* Fabr. | ad | N |
| *Cheilosia albipila* Meig. | ad | N |
| Phoridae | | |
| *Phora* sp. | ad | N |
| Pallopteridae | | |
| *Palloptera saltuum* L. | ad | N |

| | Stage | Collection method |
|---|---|---|
| Agromyzidae | | |
| *Phytobia lateralis* Macq. | ad | N |
| *P. atra* Meig. | ad | N |
| *Agromyza ambigua* Fall. | ad | N |
| Heleomyzidae | | |
| *Eccomoptera pallescens* Meig. | ad | S |
| *Oecothea fenestralis* Fall. | l, ad | S, R, N |
| Anthomyzidae | | |
| *Anthomyza cingulata* Hal. | ad | S, N |
| *Stiphrosoma sabulosum* Hal. | l, ad | S, R, E |
| Sphaeroceridae | | |
| *Pseudocollinella septentrionalis* Stenh. | ad | S |
| *Limosina* sp. | ad | E |
| Ephydridae | | |
| *Hydrellia griseola* Fall. | ad | N |
| Drosophilidae | | |
| *Scaptomyza pallida* Zett. | ad | N |
| Chloropidae | | |
| *Elachiptera tuberculifera* Corti | ad | N |
| *Aphanotrigonum trilineatum* Meig. | ad | E |
| *Oscinella cariciphila* Coll. | ad | S |
| *Chlorops pumilionis* Bjerk. | ad | N |
| Tachinidae | | |
| *Phyllomyia volvulus* Fabr. | ad | N |
| Calliphoridae | | |
| *Pollenia rudis* Fabr. | ad | N |
| *P. intermedia* Macq. | ad | N |
| *Cynomyia mortuorum* L. | ad | E, N |
| Muscidae | | |
| *Fannia postica* Stein | ad | N |
| *Mydaea* sp. | l, ad | S, R, E |
| *Helina allotalla* Meig. | ad | N |
| *H. denudata* Zett. | l, ad | S, R, N |
| *H. duplicata* Meig. | ad | N |
| *H. impuncta* Fall. | l, ad | S, R, E |
| *H. laetifica* R.D. | ad | N |
| *H. setiventris* Ringd. | ad | E |
| *Coenosia intermedia* Fall. | ad | N |
| *C. pumila* Fall. | ad | N |
| *Phaonia basalis* Zett. | ad | N |
| *Drymeia hamata* Fall. | ad | N |
| *Hydrotaea dentipes* Fabr. | ad | E |
| *H. pellucens* Portsch. | ad | N |
| *Thricops hirsutula* Zett. | ad | N |
| Anthomyiidae | | |
| *Paraprosalpia billbergi* Zett. | ad | N |
| *Hylemyia variata* Fall. | ad | N |
| *Pegohylemyia fugax* Meig. | ad | N |
| *Phorbia securis* Tiens. | ad | N |
| *Delia coarctata* Fall. | ad | N |

| | Collection method |
|---|---|
| **Araneae** | |
| Gnaphosidae | |
| Gnaphosidae sp. | S |
| Clubionidae | |
| *Clubiona* sp. | S |
| Philodromidae | |
| Philodromidae sp. | S |
| Lycosidae | |
| *Pardosa fulvipes* (Collett) | S |
| Erigonidae | |
| *Ceratinella brevipes* (Westr.) | S |
| *Dicymbium tibiale* (Bl.) | S |
| *D. nigrum* (Bl.) | S |
| *Oedothorax retusus* (Westr.) | S |
| *Tiso vagans* (Bl.) | S |
| *Gongylidiellum murcidum* Sim. | S |
| *Latithorax faustus* (Cambr.) | S |
| *Micrargus herbigradus* (Bl.) | S |
| *Erigonella hiemalis* (Bl.) | S |
| *Savignya frontata* Bl. | S |
| Linyphyiidae | |
| *Centromerita bicolor* (Bl.) | S |
| *Batyphantes gracilis* (Bl.) | S |
| *Lepthyphantes angulatus* (Cambr.) | S |
| *L. holmi* Kronest. | S |
| *Allomengea scopigera* (Grube) | S |
| **Acari Parasitiformes** | |
| Gamasina | |
| Pachylaelapidae | |
| *Pachylaelaps* cf. *laeuchlii* Schw. | S |
| Laelapidae | |
| *Hypoaspis* cf. *nolli* Karg | S |
| Phytoseiidae | |
| *Amblyseius okanagensis* (Chant) | S |
| *A. obtusus* (C.L.K.) | S |
| Ameroseiidae | |
| *Epicriopsis horridus* Kram. | S |
| Ascidae | |
| *Lasioseius berlesei* (Oudms) | S |
| *Cheirosejus borealis* (Berl.) | S |
| *Arctoseius cetratus* (Selln.) | S |
| *A. insularis* (Willm.) | S |
| Zerconidae | |
| *Mixozercon sellnicki* (Schw.) | S |
| Rhodacaridae | |
| *Rhodacarellus silesiacus* Willm. | S |
| Digamasellidae | |
| *Dendrolaelaps* sp. | S |
| Cyrtolaelapidae | |
| *Cyrtolaelaps mucronatus* (G. & R. Can.) | S |

| | Collection method |
|---|---|
| Parasitidae | |
| *Holoparasitus excipuliger* (Berl.) | S |
| *Pergamasus brevicornis* Berl. | S |
| *P. septentrionalis* (Oudms) | S |
| *P. misellus* Berl. | S |
| *P. lapponicus* Träg. | S |
| *P. runcatellus* (Berl.) | S |
| *Veigaia kochi* (Träg.) | S |
| *V. nemorensis* (C.L.K.) | S |
| *V. cerva* (Kram.) | S |
| Uropodina | |
| Uropodidae | |
| *Dinychus* sp. | S |
| Uropodidae sp. | S |
| **Acari Acariformes** | |
| Acaridei (= Astigmata) | |
| Acaridae | |
| *Schwiebea cavernicola* Vitzth. | S |
| Anoetidae | |
| *Histiostoma* cf. *feroniarum* (Dufour) | S |
| Tarsonemini (= Prostigmata, part.) | |
| Pyemotidae | |
| *Pygmephorus* sp. | S |
| *Siteroptes* sp. | S |
| Scutacaridae | |
| *Scutacarus subterraneus* Oudms | S |
| *S. crassisetus plumosus* (Paoli) | S |
| *S.* cf. *quadrangularis* (Paoli) | S |
| *S.* cf. *lapponicus* (Willm.) | S |
| Tarsonemidae | |
| *? Tarsonemus* sp. | S |
| *? Stenotarsonemus* sp. | S |
| Tetrapodili (= Prostigmata, part) | |
| Eriophyidae | |
| Eriophyidae sp. | S |
| Eleutherengona (= Prostigmata, part) | |
| Anystidae | |
| Anystidae sp. | S |
| Bdellidae sp. | |
| Bdellidae sp. | S |
| Cunaxidae | |
| *Cunaxa* sp. | S |
| Ereynetidae | |
| Ereynetidae sp. | S |
| Eupalopsellidae | |
| *Eupalopsellus* sp. | S |
| Eupodidae | |
| *Eupodes* sp. | S |
| *Cocceupodes* sp. | S |
| *Protereunetes* sp. | S |

| | Collection method |
|---|---|
| Rhagidiidae | |
| *Rhagidia* sp. | S |
| *Coccorhagidia* cf. *clavifrons* | S |
| Tetranychidae | |
| Tetranychidae sp. | S |
| Tydeidae | |
| *Tydeus* sp. | S |
| Parasitengona (= Prostigmata, part) | |
| Erythraeidae | |
| *? Hauptmannia* sp. | S |
| Endeostigmata (= Prostigmata, part) | |
| Alicorhagiidae | |
| *Alicorhagia* sp. | S |
| Nanorchestidae | |
| *Nanorchestes arboriger* (Berl.) | S |
| Pachygnathidae | |
| *Pachygnathus (Alycus) dugesi* Grdj. | S |
| Oribatei (= Crypstostigmata) | |
| Palaeacaridae | |
| *Palaeacarus histricinus* Träg. | S |
| Phthiracaridae | |
| *Steganacarus striculus* (C.L.K.) | S |
| Hypochthoniidae | |
| *Hypochthonius rufulus* (C.L.K.) | S |
| Brachychthoniidae | |
| *Brachychochthonius immaculatus* (Forssl.) | S |
| *Liochthonius sellnicki* (Thor) | S |
| Camisiidae | |
| *Platynothrus peltifer* (C.L.K.) | S |
| Damaeidae | |
| *Damaeus clavipes* (Herm.) | S |
| *D.* cf. *verticillipes* Nic. | S |
| Carabodidae | |
| *Carabodes areolatus* Berl. | S |
| Tectocepheidae | |
| *Tectocepheus sarekensis* Träg. | S |
| Oppiidae | |
| *Oppia minus* (Paoli) | S |
| *O. nova* (Oudms) | S |
| Suctobelbidae | |
| *Suctobelba subtrigona* (Oudms) | S |
| *S. falcata* Forssl. | S |
| Oribatulidae | |
| *Oribatula tibialis* (Nic.) | S |
| *Hemileius initialis* (Berl.) | S |
| *Scheloribates laevigatus* (C.L.K.) | S |
| Chamobatidae | |
| *Chamobates cuspidatus* (Mich.) | S |
| Ceratozetidae | |
| *Trichoribates trimaculatus* (C.L.K.) | S |
| Parakalumnidae | |
| *Neoribates aurantiacus* (Oudms) | S |

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